Advances in MARINE BIOLOGY

VOLUME 53

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VOLUME FIFTY THREE

ADVANCES IN MARINE BIOLOGY

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Edited by

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THE EVOLUTIONARY ECOLOGY OF OFFSPRING SIZE IN MARINE INVERTEBRATES

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Abstract

Intraspecific variation in offspring size is of fundamental ecological and evolutionary importance. The level of provisioning an organism receives from its mother can have far reaching consequences for subsequent survival and performance. In marine systems, the traditional focus was on the remarkable variation in offspring size among species but there is increasing focus on variation in offspring size within species. Here we review the incidence and consequences of intraspecific offspring-size variation for marine invertebrates.

Offspring size is remarkably variable within and among marine invertebrate populations. We examined patterns of variation in offspring size within populations using a meta-analysis of the available data for 102 species across 7 phyla. The average coefficient of variation in offspring size within populations is 9%, while some groups (e.g., direct developers) showed much more variation (15%), reflecting a fourfold difference between the largest and smallest offspring in any population.

Offspring-size variation can have for reaching consequences. Offspring size affects every stage of a marine invertebrate’s life history, even in species in which maternal provisioning accounts for only a small proportion of larval nutrition (i.e., planktotrophs). In species with external fertilization, larger eggs are larger targets for sperm and as such, the sperm environment may select for different egg sizes although debate continues over the evolutionary importance of such effects. Offspring size affects the planktonic period in many species with planktotrophic and lecithotrophic development, but we found that this effect is not universal. Indeed, much of the evidence for the effects of offspring size on the planktonic period is limited to the echinoids and in this group and other taxa there is variable evidence, suggesting further work is necessary. Post-metamorphic effects of offspring size were strong in species with non-feeding larvae and direct development: bigger offspring generally have higher post-metamorphic survival, higher growth rates and sometimes greater fecundity. Although there is limited evidence for the mechanisms underlying these effects, the size of post-metamorphic feeding structures and resistance to low-food availability appear to be good candidates. There was limited evidence to assess the effects of offspring size on post-metamorphic performance in planktotrophs but surprisingly, initial indications suggest that such effects do exist and in the same direction as for species with other developmental modes. Overall, we suggest that for direct developers and species with non-feeding larvae, the post-metamorphic effects of offspring size will be greatest source of selection.

Offspring-size variation can arise through a variety of sources, both within and among populations. Stress, maternal size and nutrition, and habitat quality all appear to be major factors affecting the size of offspring, but more work on sources of variation is necessary. While theoretical considerations of offspring size can now account for variation in offspring size among mothers, they struggle to account for within-brood variation. We suggest alternative approaches such as game theoretic models that may be useful for reconciling within-clutch variation. While some of the first theoretical considerations of offspring size were based on marine invertebrates, many of the assumptions of these models have not been tested, and we highlight some of the important gaps in understanding offspring-size effects. We also discuss the advantages of using offspring size as a proxy for maternal investment and review the evidence used to justify this step.

Overall, offspring size is likely to be an important source of variation in the recruitment of marine invertebrates. The quality of offspring entering a population could be as important as the quantity and further work on the ecological role of offspring size is necessary. From an evolutionary standpoint, theoretical models that consider every life-history stage, together with the collection of more data on the relationship between offspring size and performance at each stage, should bring us closer to understanding the evolution of such a wide array of offspring sizes and developmental modes among species.

1. INTRODUCTION

Offspring size is a trait of fundamental interest to evolutionary biologists and ecologists. Offspring size, for our purposes, will be defined as the volume of a propagule once it has become independent of maternal nutritional investment. According to this definition, the size of freely spawned egg is the appropriate measure of offspring size but the size of a direct developing snail egg before the embryo has ingested nurse eggs is not. The enormous range of offspring sizes observed among species, even closely related ones (Fig. 1.1), has long fascinated biologists as to the selection pressures that led to such divergent sizes (Lack, 1947). Offspring size is of particular interest because while it has fitness consequences for both the offspring and mother, selection acts to maximize maternal fitness only (Bernardo, 1996). Thus, mother and individual offspring may be in conflict with regards to the strategy that maximizes fitness (Einum and Fleming, 2000). Similarly ecologists have long been interested in the role of maternal investment in population dynamics (Bagenal, 1969) and for most organisms, offspring size is the sole source of maternal investment. If we hope to understand the evolutionary pressures acting on offspring size, then we must first determine the ecological consequences of this variation within species. In his excellent review of propagule size effects, Bernardo (1996, pp. 219–220) points out 'The ecological and evolutionary implications of variation in propagule size are evaluated by selection and modelled by theoreticians as a within-population variance component. . . . It is at the within- to among-population (intraspecific) level that we should seek evidence of the ecological role and evolutionary dynamics of propagule size and their relationship to parental phenotypes . . .'. The goals of evolutionary

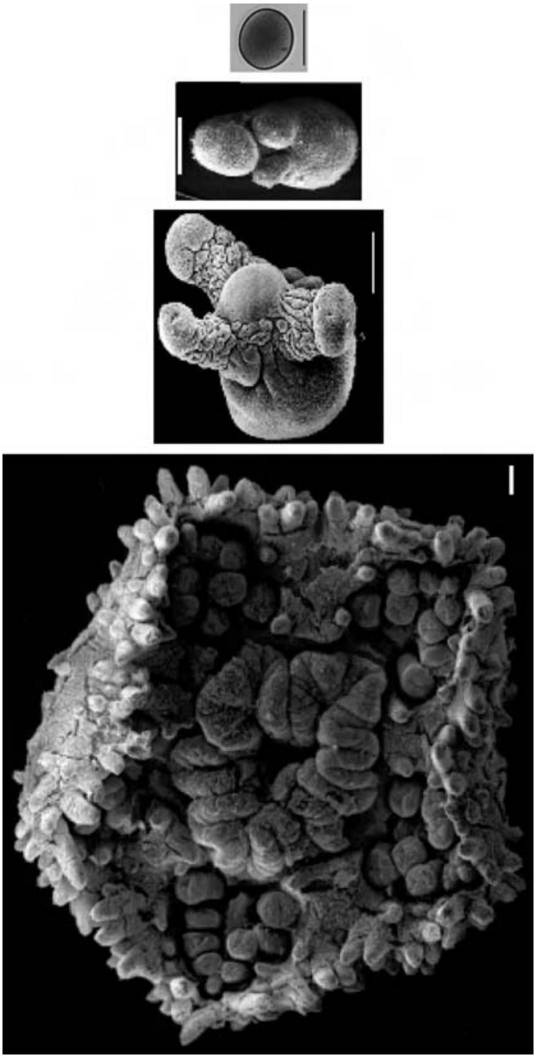


Figure 1.1 Micrographs of the offspring from four species of closely related Australian sea stars within the Asterinidae, left to right is the brooded *Parvulustra parvivipara*, the benthic lecithotroph *Parvulustra exigua*, the lecithotrophic broadcast spawner *Meridiastra calcar* and the planktotrophic broadcast spawner *Patiriella regularis*. Scale bar is 100 μm and note that for *P. parvivipara*, the scale bar is half the size of the others. Micrographs courtesy of Maria Byrne.

biology and ecology can be achieved by the same means then—the examination of the effects of offspring size within individual species.

Marine invertebrates have one of the most diverse and striking range of offspring sizes exhibited among species. For example, latitudinal patterns in offspring size were noted more than 50 years ago by Thorson (1950). Consequently, one of the first attempts at modelling offspring size was done with marine invertebrates in mind (Vance, 1973a). In their excellent review of *Conus* life-history strategies, Kohn and Perron (1994) concluded that, '. . . egg size is the single most important attribute of understanding (1) reproductive energetics; (2) the temporal patterns of embryonic development and larval biology; (3) dispersal potential, which is tightly linked to (1) and (2) but is an evolutionary "byproduct". . .'. However, despite a long fascination with offspring-size evolution, intraspecific variation in offspring size and its effects have only recently been examined in detail. One of the first studies on intraspecific offspring-size variation in marine invertebrates was done in the late 1970s (Turner and Lawrence, 1977), but for the most part earlier work tended to focus on the effects of interspecific variation (e.g., Berrill, 1935; Dickie *et al.*, 1989; Emlet *et al.*, 1987; Hoegh-Guldberg and Pearse, 1995; Staver and Strathmann, 2002; Steele, 1977 but see Kohn and Perron, 1994). Indeed, it has been our personal experience that people are surprised when we present remarkably high levels of variation in offspring size within species. However, in both the terrestrial and marine literature, offspring-size studies have increasingly focused on within-species variation. We believe that this is appropriate: as pointed out by Bernardo (1996), it is inappropriate to use interspecific studies to infer ecological effects or evolutionary transitions without controlling for species relationships (for detailed discussion, see Harvey and Pagel, 1991). More importantly, intraspecific variation in offspring size has the potential to dramatically change our view of the dynamics of marine invertebrate populations. Settling larvae are traditionally viewed (and modelled) as being homogenous in their chances of recruiting and their post-settlement performance (Eckman, 1996; Vance, 1973). However, it has become clear that settling larvae vary greatly in their potential to survive and grow to reproduction. Exposure to pollutants, increased swimming durations or larval activity levels and larval nutrition can strongly affect post-metamorphic performance in a range of taxa (Highsmith and Emlet, 1986; Marshall *et al.*, 2003b; Ng and Keough, 2003; Pechenik *et al.*, 1998, 2001; Phillips and Gaines, 2002; Wendt, 1998). Many of these 'carry-over' effects are thought to be mediated by variation in larval energetic reserves (Bennett and Marshall, 2005; Wendt, 2000) such that if larger offspring have more energetic reserves than smaller offspring, then similar effects would be expected. Thus, offspring size could be an important source of variation in larval quality and, consequently, variation in recruitment. Traditionally, we have viewed marine invertebrate populations as being strongly affected by the *quantity* of larvae entering a population; intraspecific variation in offspring could also mean that the *quality* of larvae could have equally important effects.

In light of the evolutionary and ecological importance of intraspecific variation in offspring size, we have several aims for this review:

1. Document and quantify the amount of variation in offspring size within marine invertebrate species.
2. Review the known effects of offspring size across the various life-history stages of marine invertebrates.
3. Identify the common sources of intraspecific variation in offspring size within and among marine invertebrate populations.
4. Summarize the findings of the theoretical literature on offspring-size effects in marine invertebrates.
5. Identify the key knowledge gaps that currently limit our understanding of the ecological and evolutionary consequences of offspring-size variation.

Our first aim represents an attempt to highlight the fact that offspring sizes are extremely variable within and among marine invertebrate populations. Our second aim is a first attempt at integrating the various findings for different life-history stages, and we hope to demonstrate that selection is likely to act on offspring size across multiple, if not all, life-history stages. We will demonstrate that offspring-size variation can have pervasive and important effects on performance at each life-history stage, so the next obvious step is to identify some of the sources of this variation. We will then examine whether current theoretical considerations of the issue match our empirical findings and the problems associated with various approaches. We will then attempt to identify the appropriate next steps in understanding the evolutionary and ecological consequences of offspring-size variation within species.

2. HOW VARIABLE IS OFFSPRING SIZE WITHIN SPECIES?

2.1. Meta-analysis of the literature

In this section, we summarize the degree of variation in offspring sizes from species, from a range of taxa and from 7 phyla (including 35 orders, 58 families and 102 species) and compare the relative variation from each of the three major developmental modes (planktotrophic, lecithotrophic and direct development). Here, lecithotrophic is used as a general term for non-feeding larvae; however, it is recognized that not all non-feeding larvae are necessarily 'yolk feeding'. Facultative planktotrophs (species that can feed but do not necessarily need to in order to become competent to metamorphose McEdward, 1997) are considered to be lecithotrophic for the purposes of this chapter. For the purposes of our analysis and our review more generally, we define 'direct development' here as any development whereby the offspring are fully formed juveniles independent of maternal nutrition sources (although not necessarily maternal nutrition: these juveniles may still be utilizing maternal yolk reserves). The two groups with planktonic development were further partitioned into internal and external fertilizers. We compiled data on variation in offspring size from the available literature and from our own unpublished data (see Appendix). The most commonly reported measure of offspring size was length of embryos/newly hatched larvae or egg diameter. For a number of species (especially the gastropods), the sizes of a range of different developmental stages were available. Because we were interested in variation in total maternal investment per offspring, the measure that best reflected this investment was utilized. For example, for gastropods that fed on nurse eggs prior to hatching, we utilized measures of size and variation in size for newly hatched juveniles rather than those parameters for newly laid eggs (cf. Kohn and Perron, 1994). We used data for species only where the eggs of two or more individuals were measured. Often the source of the variation (among broods or within broods) was not reported and so for the majority of cases we cannot determine the principal source of the variation. Data on offspring size were compiled from studies that collected females from the same population and in most cases the same time, although in some cases data were compiled from a single reproductive season. Many other studies were excluded because no details were provided of the numbers of individuals on which the summary of offspring size was based. Egg volume was also a commonly reported measure, although we did not include data using this parameter in most of the analyses because variance [and more importantly, coefficients of variation (CVs)] in diameter and volume are not equivalent and, more importantly, do not scale linearly. Thus, we would discourage the approach used by Einum and Fleming (2002) whereby CVs in egg volume and diameter are pooled because this could introduce biases to the analysis.

To overcome the problems associated with traditional comparative analyses (i.e., treating individual species as replicates), we used the method of higher node contrasts (Harvey and Pagel, 1991). We tested the effects of developmental type and reproductive mode at the species, family and order level. The effects of developmental type (direct, lecithotrophic and planktotrophic as different levels) on CVs of offspring size within populations were tested with ANOVA. For the planktotrophs and lecithotrophs, we also compared the CV of offspring size within developmental types for two reproductive modes: internal and external fertilization.

The level of within-population variability in offspring size differed considerably between species, with CVs ranging from 0.7% to 51% (Fig. 1.2). The average CV across the entire set of species was approximately 9% and is

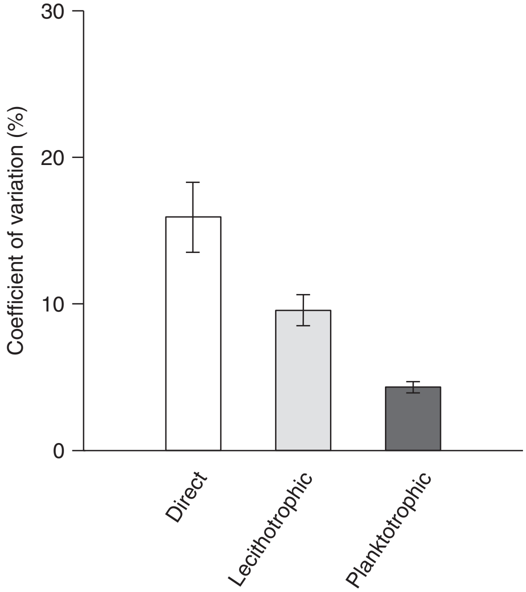


Figure 1.2 Mean (±SE) CV for offspring size within populations of marine invertebrates. Data are compiled from the literature for three developmental types: direct developers, lecithotrophic and planktotrophic.

similar to previous averages reported for *Conus* species (Kohn and Perron, 1994). This level of variation in diameter means that within any group of eggs, about a third of all the offspring will be 25% larger or smaller in volume than the average size and about 5% will be 50% larger or smaller in volume than the average size. Note that our calculations assume a normal distribution of egg sizes, and the data appear to reflect this distribution. Intra-population variation in offspring size varied strongly with developmental mode, and this pattern was consistent at all taxonomic levels that were tested (analysis using species, $F_{2,99} = 27.13$; families, $F_{2,64} = 24.6$; orders, $F_{2,40} = 22.51$; all $P < 0.001$; and all pairwise comparisons $P < 0.001$). Variation was greatest in the direct developers, least in planktotrophs and intermediate in lecithotrophs (Fig. 1.2).

For the direct developers only, a CV of 14% means that about a third of all the offspring will be 48% larger or smaller in volume than the average size and 5% of offspring will be more than twice the average size. Put in another way, this means a fourfold difference between the smallest 5% and largest 5% of individuals within any one population. These figs. show that there is an impressive range of offspring sizes being produced within any one population of marine invertebrate. Given that the size of direct developers was, on average, greater than indirect developers, we were concerned that the effects of developmental type were confounded with offspring size. Generally, however, CV was not correlated with offspring size within all three reproductive modes (direct developers: $R^2 = 0.104$, $n = 20$, $P = 0.165$; planktotrophs: $R^2 = 0.03$, $n = 39$, $P = 0.3$; lecithotrophs: $R^2 = 0.02$, $n = 43$, $P = 0.8$).

Within the lecithotrophs, internal fertilizers had higher levels of within-population variation in offspring size than external fertilizers ($F_{1,37} = 10.85$, $P = 0.002$, Fig. 1.3). For planktotrophs, there was no effect of fertilization mode on the level of within-population variation in offspring size ($F_{1,40} < 0.01$, $P = 0.99$, Fig. 1.3) despite the fact that the power to detect an effect similar to that seen for non-feeding larvae was high at 0.9.

Given the strong effects of relatively small differences in offspring size discussed later in this chapter, it seems that among all the developmental modes, the quality and performance of offspring will be highly variable within any single population. Our results suggest that the relative importance of larval quality and quantity for subsequent population dynamics will depend on developmental type. Overall, variation in offspring size in direct developers was very high—thus, larval quality may be particularly important for explaining variation in recruitment in this group because different individuals can vary markedly in quality.

It is difficult to speculate as to the cause of the pronounced differences in offspring-size variation between developmental and fertilization modes as a

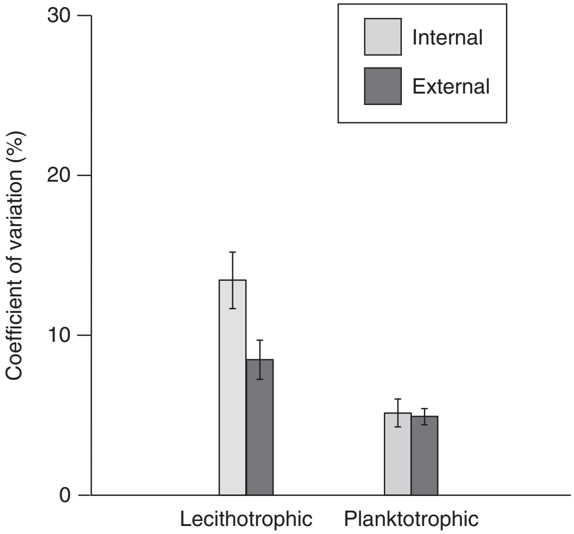


Figure 1.3 Mean (±SE) CV for offspring size within populations for marine invertebrates with planktotrophic or lecithotrophic development. The shaded bars represent species with external fertilization and open bars represent species with internal fertilization.

number of factors could be driving this effect. However, it is worth noting that there appears to be a strong, negative relationship between the dispersal potential of offspring and variation in offspring size, the most variation in the non-dispersing direct developers through to internally fertilized lecithotrophs and the least variation in the highly dispersive externally fertilized planktotrophs. Further work distinguishing between the two sources of intrapopulation variation (within brood and among individuals; e.g., Kohn and Perron, 1994) may shed light on the causes behind the systematic differences between the various developmental groups.

3. EFFECTS OF OFFSPRING SIZE

From our analysis of within-population offspring-size variation, it is clear that offspring sizes can be highly variable within species and populations. In this section, we review the effects of offspring-size variation on each of the major life-history stages across the various developmental modes. We do not consider the differential benefits to mothers of brooding smaller versus larger offspring but note that in some other groups this can be a major factor (Sakai and Harada, 2001). Unfortunately, there are far too few data on this important issue in marine invertebrates and so we focus on each of the life-history stages following the release of gametes/offspring.

3.1. Fertilization

In Thorson's consideration of free-spawning invertebrates, he concluded that '. . . . failure of insemination, cannot explain the enormous waste [of eggs] found in most marine invertebrates during development. The heavy waste takes place after fertilisation, during the free swimming pelagic life' (Thorson, 1950). Since then it has become clear that fertilization is not assured in free-spawners, and the production of zygotes can be a potentially limiting factor in the population dynamics of some species (Levitan, 1991, 1995; Levitan and Petersen, 1995; Levitan *et al.*, 1992; Pennington, 1985; Yund, 2000). Here we define 'free-spawning' as the release of both sperm and eggs into the water column. While free-spawning has alternatively been termed 'broadcast spawning' (Byrne *et al.*, 2003; Oliver and Babcock, 1992), we prefer the term free-spawning, partly because in many species, eggs are not 'broadcasted' into the water column but remain in a viscous matrix near the spawning female (Marshall, 2002; Thomas, 1994; Williams *et al.*, 1997). However, we should note that we separate free-spawning/broadcast spawning from species where only sperm are shed into the water column while eggs are retained (sometimes termed 'spermcast spawning'; Pemberton *et al.*, 2003). The principal factor determining the fertilization rate of spawned eggs is the collision rate between eggs and sperm (Vogel *et al.*, 1982). The collision rate between eggs and sperm is affected by a range of factors, but most important is the concentration of sperm present (Marshall *et al.*, 2000; Styan, 1998). Thus, any factors that change the amount of sperm present in the water column will affect female fertilization success and, accordingly, the density of spawning males and local hydrodynamic conditions will strongly affect fertilization rates in the natural environment (Denny and Shibata, 1989; Denny *et al.*, 1992; Franke *et al.*, 2002; Lasker *et al.*, 1996; Levitan, 1991; Levitan *et al.*, 1992; Marshall, 2002; Marshall *et al.*, 2004b; Mead and Denny, 1995; Yund, 1990). Given that sperm can quickly dilute to ineffective concentrations in the field (Babcock *et al.*, 1994; Denny and Shibata, 1989), a number of adaptations exist that enhance fertilization success in free-spawners and most relevant to the discussion here is the effect of egg size.

Larger eggs present a larger 'target' for sperm and are therefore more likely to be contacted within a given period of time than smaller sperm (Levitan, 1996a; Marshall *et al.*, 2002; Styan, 1998; Vogel *et al.*, 1982). Both in the laboratory and the field, when sperm are scarce, larger eggs are more likely to be fertilized than smaller eggs (Levitan, 1996a,b; Marshall and Keough, 2003; Marshall *et al.*, 2002). However, when sperm are abundant, larger eggs are more likely to suffer polyspermy than smaller eggs either because they are more likely to be contacted by multiple sperm before they have formed a block to polyspermy or because such blocks are slower (Marshall and Keough, 2003; Marshall *et al.*, 2002; Millar and Anderson, 2003; Styan, 1998). Therefore, under sperm-limiting conditions, larger eggs are more likely to be successfully fertilized, while under polyspermy conditions, smaller eggs are more likely to be fertilized. Debate continues about the prevalence of sperm limitation and polyspermy under natural conditions, but it is clear that both can occur simultaneously in the same spawning population (Brawley, 1992; Franke *et al.*, 2002; Marshall, 2002).

The effects of egg size on fertilization rate have led to speculation about the evolution of egg sizes of free-spawning marine invertebrates and the evolution of anisogamy (Levitan, 1993, 1996a; Podolsky, 2001; Podolsky and Strathmann, 1996). It has been suggested that in habitats that are conducive to sperm-limiting conditions, larger eggs have evolved relative to species in habitats where sperm limitation is unlikely (Levitan, 1998, 2002). More broadly, Levitan argues that the evolution of egg size in marine invertebrates will be strongly influenced by the pre-zygotic selection associated with fertilization. In contrast, Podolsky and Strathmann (1996) argue that the benefits of increased egg size for fertilization will be outweighed by the reduction in fecundity associated with this increase. Furthermore, they argue that post-zygotic selection (i.e., the effects of offspring size on developmental and post-metamorphic performance) will also shape offspring size and overall pre-zygotic selection (i.e., effects on fertilization alone) will be less important (Podolsky and Strathmann, 1996). This debate has been broadened by the discussion of the effects of egg accessory structures. Many invertebrates produce eggs that have large accessory structures such as jelly coats or follicle cells surrounding the eggs (reviewed in Podolsky, 2001). It has been argued that, as accessory structures are energetically inexpensive relative to egg material (Bolton and Thomas, 2000), any selection to increase egg target size will result in an increase in these structures rather than the egg cell itself (Podolsky, 2001, 2002; Podolsky and Strathmann, 1996). Farley and Levitan (2001) propose that despite the effects of accessory structures on fertilization, there will still be substantial selection on egg size due to fertilization effects. Podolsky (2001) raises the interesting possibility that egg accessory structures may mediate sperm–egg interactions in ways other than just size (e.g., increase the variance in sperm arrival times, thereby reducing polyspermy); it will be interesting to determine if this is indeed the case. Overall, this debate remains unresolved. Nevertheless it seems unlikely that pre-zygotic selection on egg size will be the sole force in the evolution of egg size in free-spawners, especially given the post-zygotic effects of egg size outlined later in this chapter.

An important consequence of the size-dependent fertilization of eggs is that under different sperm concentrations, the same brood of unfertilized eggs will produce zygotes of different sizes. At low sperm concentrations larger zygotes will be produced, but if that same brood is exposed to a high sperm concentration then (because of polyspermy effects) smaller, viable zygotes will be produced (Levitan, 1996a,b; Marshall and Keough, 2003; Marshall *et al.*, 2002). Therefore, free-spawning marine invertebrates appear to be unusual in that the size distribution of zygotes is a product not only of maternal investment but also of the local 'sperm environment'. This raises the interesting possibility that free-spawning males and females may be in conflict at fertilization whereby male fitness is maximized by a strategy that may reduce female fitness (Franke *et al.*, 2002). Finally, size-dependent fertilization means that producing offspring of optimal size is further complicated in free-spawning species because an additional 'layer' of size-dependent selection occurs at fertilization. For example, because free-spawning mothers may be competing for limiting sperm (Marshall and Evans, 2005), selection at this stage could act to increase optimal egg size (and thus competitive ability) but selection at another stage could act to decrease optimal egg size (i.e., size-independent mortality at settlement). Clearly, the effects of egg size at fertilization in free-spawners have the potential to influence egg size evolution; further research on the effects of offspring size across the entire life history of an organism will determine the relative strength of selection on egg size at each stage.

3.2. Development

Our view of the effects of offspring size on developmental time (time to a functional stage such as feeding or metamorphic competence) has been shaped largely by the early models of Vance (1973a,b). In both of Vance's original papers, it is assumed that the length of the pre-feeding period (or λ) increased with offspring size, and that the length of feeding period (ρ) decreased with offspring size. For non-feeding larvae with planktonic development, this means that the total planktonic period should be *positively* correlated with egg size because ρ is zero (although Vance restricted his considerations for $S \leq 1$). For feeding larvae, Vance (1973a, p. 342) made another assumption that the influence of egg size on λ was much smaller than its influence on ρ (in terms of the model $P \gg 1$) and so concluded that for planktotrophic species, egg size should be *negatively* correlated with planktonic period. Vance's models predicted that only very small or very large offspring should be selected and since then various modifications of the model have been made that better approximate the distribution of egg sizes observed in nature (Levitan, 1993, 2000; Podolsky and Strathmann, 1996; Styan, 1998). Since Vance's work, the assumptions that increases in egg size result in decreases in the planktonic period for feeding larvae and increases in the planktonic period of non-feeding larvae have become accepted in theoretical considerations of the topic and some conceptual works (Levitan, 2000; Ramirez-Llodra, 2002 but see Strathmann, 1977). For direct developers, there has been little speculation on the effects of offspring size on subsequent development but some general offspring-size models do assume a relationship between offspring size and developmental time (Sargent *et al.*, 1987). In this section, we review the available evidence for each of these assumptions.

3.2.1. Planktotrophs

3.2.1.1. Pre-feeding period There are very few studies examining the effects of egg size on the pre-feeding period alone in marine invertebrates. In one of the few studies to examine the effects of intraspecific variation in egg size on pre-feeding developmental time, McLaren (1965, 1966) showed that larger eggs took longer time to hatch than smaller eggs for the copepod *Pseudocalanus minutus*. Similarly in another copepod, Lonsdale and Levinton (1985) found across four populations that female *Scottolana cnadensis* from the population that produced the largest eggs also produced eggs that took the longest time to hatch into nauplii. In contrast, Jones *et al.* (1996) found no correlation between egg size and embryonic developmental period among populations in the nudibranch *Adalaria proxima*. Among species, the effect of egg size on the length of pre-feeding period is also unclear. Dickie *et al.* (1989) compared the length of pre-feeding periods among strongylocentrotid sea urchin species and found no influence of egg size, although only one clutch from each species was used in this study. In a study across 20 different species with feeding larvae from a number of phyla, Staver and Strathmann (2002) found that the time until first swimming was positively correlated with egg size, but within individual groups (Urochordates, Echinoderms and Spiralia), the effects of egg size were less clear and were limited by small sample sizes. Some of the best evidence comes from Kohn and Perron's study showing a positive relationship between the pre-feeding (pre-hatching) period and egg size among species of *Conus* (Kohn and Perron, 1994).

3.2.1.2. Entire planktonic period: Interspecific comparisons Emlet (1995) considered the relationship between overall length of the developmental period (from the fertilization of eggs to metamorphic competence) of 28 echinoids with feeding larvae and 5 echinoids with non-feeding larvae. He found that the larval period decreased with increased egg size across both developmental modes (Emlet, 1995). Extending Emlet's work, Levitan (2000) examined the relationship between egg size and planktonic duration for 37 echinoid species, all with feeding larvae. Again, it was found that those species with larger eggs had a shorter planktonic period than those with smaller eggs. It should be noted that for both studies, developmental periods were first adjusted with Q_{10} values so that comparisons could be made across species that occurred at different water temperatures. Before adjusting for temperature, Emlet (1995) found no relationship between egg size and larval developmental period. Importantly, Levitan (2000) found that the relationship between egg size and planktonic period was not linear (as assumed by Vance, 1973a,b), rather, it was curvilinear with initial increases in egg size resulting in a large decrease in the planktonic period; however, with increased egg size the concomitant reduction in planktonic period was less.

Analysing the available data for Asteroidea (Echinodermata), across the planktotrophs and lecithotrophs, there is the expected relationship between egg size and planktonic period (Emlet *et al.*, 1987). However, the effects of egg size on developmental rate within feeding larvae alone are less clear. Using Q_{10} values of 2, there is a significant negative correlation between egg size and planktonic period but using values of 3–3.6 (typical values for echinoderm larvae, see Emlet, 1995), there is no significant correlation between egg size and planktonic period. Similar results were reported by Hoegh-Guldberg and Pearse (1995).

There have been far fewer studies examining the effects of egg size on the planktonic period of feeding larvae that are not focused on echinoderms. Kohn and Perron (1994) showed a strong negative relationship between the minimum planktonic period and egg diameter in *Conus* (Fig. 1.5). Havenhand (1993) compared the developmental time (again standardizing for differences in temperature) of opisthobranch molluscs with a range of different egg sizes. He found that across developmental modes (planktotrophic and lecithotrophic) there was a strong negative relationship between egg size and developmental time, with lecithotrophs having a shorter developmental period (Havenhand, 1993). However, when lecithotrophs and planktotrophs are considered separately, there is no relationship between egg size and developmental time for either group (planktotrophs: $R^2 = 0.01$, $n = 18$, $P > 0.5$; lecithotrophs: $R^2 = 0.269$, $n = 13$, $P = 0.069$). This suggests that apart from the broad differences between planktotrophs and lecithotrophs, there is no effect of egg size on developmental time in this group despite the comparisons being made across a broad range of egg sizes within each group (e.g., for planktotrophs between 65 and 149 μm; Fig. 1.4). Further studies on other, non-echinoid groups are necessary to determine if the relationship between egg size and the planktonic period for feeding larvae is applicable to other groups of organisms.

We compiled the data from the review by Kupriyanova *et al.* (2001) on serpulimorph polychaetes, to examine the relationship between egg size and developmental time and to be conservative, we compared our results across two values of Q_{10}: 2 and 3.6 (the results were qualitatively independent of the Q_{10} that was used). Once again, the polychaete data do not resemble the data on echinoids. Across feeding and non-feeding larvae, developmental

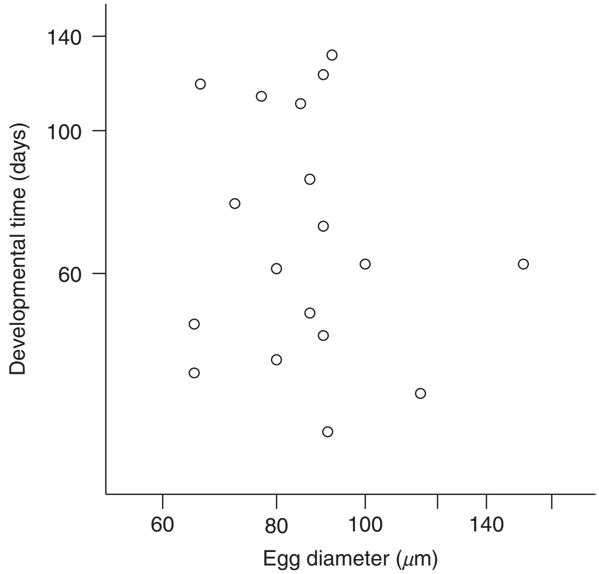


Figure 1.4 Relationship between egg size and developmental time (adjusted to development at 10 °C using Q_{10} values) for opisthobranch molluscs with planktotrophic larvae, each point represents a single species. Data taken from Havenhand (1993), note the log scale. Developmental time is defined here as the time from egg release/fertilization through to metamorphic competence.

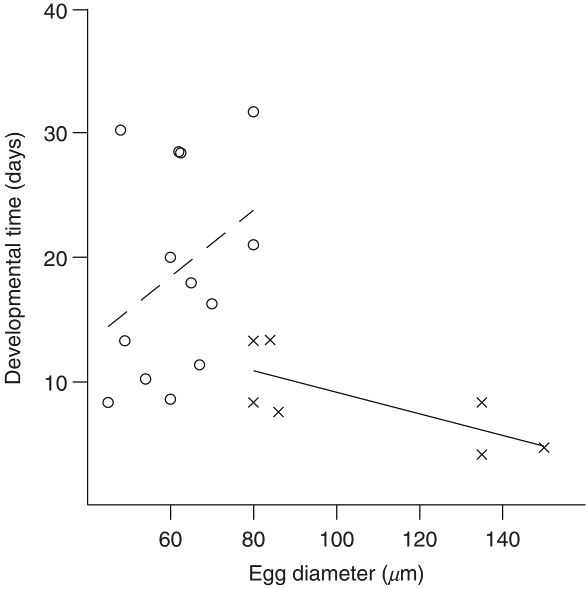


Figure 1.5 Relationship between egg size and developmental time (adjusted to development at 20 °C using Q_{10} values) for serpulimorph polychaetes with planktotrophic (as indicated by circles and the dashed line) or lecithotrophic (as indicated by the crosses and solid line). Data taken from Kupriyanova *et al.* (2001), and developmental time was defined as time taken to reach metamorphic competence.

time does decrease with increasing egg size ($Q_{10} = 2$, $R^2 = 0.199$, $n = 20$, $P = 0.048$; $Q_{10} = 3.6$, $R^2 = 0.212$, $n = 20$, $P = 0.041$). However, there is no statistically significant relationship between egg size and developmental time ($Q_{10} = 2$, $R^2 = 0.299$, $n = 13$, $P = 0.053$; $Q_{10} = 3.6$, $R^2 = 0.154$, $n = 13$, $P = 0.184$) when planktotrophs are examined on their own (Fig. 1.5). In fact, there is almost a positive relationship between egg size and developmental time in planktotrophic polychaetes (Fig. 1.6). Our discussion of interspecific patterns that have been adjusted using Q_{10} values should be tempered with the fact that such measures that assume Q_{10} values remain constant across temperature ranges, a condition that is unlikely in some instances (Hoegh-Guldberg and Pearse, 1995). This further emphasizes the advantages of examining offspring-size effects within rather than among species.

For holoplanktonic species, the pattern appears to be similar. Guisande and Harris (1995) found that hatching success and naupliar survival under conditions of starvation were positively correlated with egg size in the copepod *Calanus helgolandicus*. Similarly, Lonsdale and Levinton (1985) found, among populations, that egg size was positively correlated with naupliar survival under low-food conditions but not high-food conditions.

In summary, it appears that for planktotrophic larvae, the echinoids and *Conus* gastropods are the only groups where egg size consistently affects the

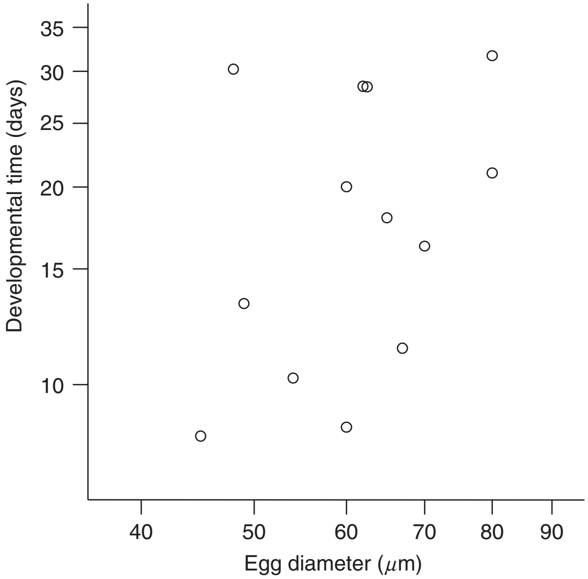


Figure 1.6 Relationship between egg size and developmental time (adjusted to development at 20 °C using Q_{10} values) for serpulimorph polychaetes with planktotrophic larvae. Data taken from Kupriyanova *et al.* (2001), note the log scale. Developmental time is defined here as the time from egg release/fertilization through to metamorphic competence.

planktonic period, whereas for other groups there appears to be little support for the idea that larvae from smaller eggs require longer time to develop. This may be because the influence of egg size on the pre-feeding period is actually much larger than has previously been assumed, potentially balancing out (or perhaps even overcoming in the case of polychaetes) the effects of egg size on the length of the feeding period.

*3.2.1.3. **Entire planktonic period: Intraspecific comparisons*** The number of studies on feeding larvae that examine the effect of egg size on developmental time *within* species is severely limited. Bertram and Strathmann (1998) found a small effect of maternal source habitat (and thus egg size) on the developmental rate of larvae of the urchin *Strongylocentrotus droebachiensis* fed in the laboratory. However, Meidel *et al.* (1999) found that increased egg size in *S. droebachiensis* resulted in an increase in the rate of metamorphosis for larvae fed high but not low food rations. George *et al.* (1990) found that larvae from larger eggs were competent to settle sooner than larvae from smaller eggs in the echinoids *Arbacia lixula* and *Paracentrotus lividus*, although these comparisons are based on mothers from different sites.

While examinations of the effect of natural variation in egg size are rare, several studies have examined the effects of manipulating egg size.

Hart (1995) halved the size of developing eggs in the echinoid *S. droebachiensis* with no effect on time to metamorphose and only a small effect on juvenile size. Surprisingly, he found no effect of egg size on the time taken to progress through the larval stage despite strong effects on larval feeding rates, with larvae coming from halved eggs having lower clearance rates than those from unmanipulated eggs. Sinervo and McEdward (1988) manipulated the size of *S. droebachiensis* eggs and found that egg size strongly affected developmental rate with larvae coming from smaller eggs taking longer time to reach metamorphosis than larvae from larger eggs.

3.2.2. Non-feeding larvae

3.2.2.1. Interspecific comparisons Berrill's (1935) examination of the effect of egg size on developmental time (measured as time to swimming) in ascidians is perhaps the best-known example of the effects of offspring size on developmental rate in non-feeding larvae. Species with larger eggs took longer to develop than species with smaller eggs at the same temperature. Interestingly, there are very few other examinations of the effects of offspring size on developmental time in this group. Staver and Strathmann (2002) found that egg size and time to swimming appeared to positively (although statistically non-significantly) correlated among three species of Urochordate. In contrast, Emlet *et al.* (1987) found a strong, positive correlation between egg size and planktonic period across 36 species of non-feeding asteroid larvae.

3.2.2.2. Intraspecific comparisons There are very few examinations of the intraspecific effects of offspring size on developmental time or planktonic period in species with non-feeding larvae. Isomura and Nishimura (2001) found that larger larvae had longer lifetimes (measured as the time from the free-swimming stage to when the larvae died and therefore probably exceeds the time taken to become metamorphically competent) than smaller larvae within three species of pocilloporid corals. More recently, Marshall and Bolton (2007) showed that egg size strongly affected time until hatching in two species of ascidian (*Ciona intestinalis* and *Phallusia obesa*) and the sea urchin *Heliocidaris erythrogramma*. The magnitude of the effects of egg size on developmental time in this study was surprising, with small increases in egg size dramatically increasing developmental time (e.g., for *Ciona* an approximately 4% increase in offspring size resulted in a 15% increase in developmental time). This has some interesting implications for the way in which egg size evolution is modelled. As discussed above, Vance's (1973a) model assumed that the effects of egg size variation on the feeding period were much larger than its effects on the pre-feeding period, so any increase in egg size would result in a large decrease in the feeding period and only a small increase in the pre-feeding period. Later models even removed the effects of egg size on the pre-feeding period, regarding it as constant (e.g., Levitan, 2000, p. 178). The effect of egg size on the pre-feeding period should not be assumed to be substantially less than its effect on the feeding period. Given the lack of an effect of egg size on total developmental time discussed above, we suggest that the effects of egg size on the pre-feeding period may partially balance the effects of egg size on the feeding period, thereby obscuring any relationship between egg size and time to metamorphic competence. Alternatively, differences in the size at metamorphosis among species may also be obscuring any egg size–feeding period relationship in planktotrophs (Strathmann, 1977).

Offspring size can also affect larval behaviour. Our own work on brooding species has shown that larger larvae actually spend longer in the plankton than smaller larvae, at least for species with brooded larvae (Marshall and Keough, 2003). However, this is not due to differences in the developmental time of larvae, indeed the larvae of each of the species in our study were capable of settlement immediately (Marshall and Keough, 2003). The differences appear to be due to the fact that larger larvae are more ‘choosy’ with respect to settlement surfaces. Hence for any given larva, the larval period is a product of the availability of suitable substrates and the size of the larva.

The effect of larval size on the developmental time/settlement behaviour of non-feeding larvae has some interesting implications for variation in the dispersal potential of this group. All else being equal, larger larvae will have greater dispersal than smaller larvae. Thus, if a mother produces offspring of variable size, then she will also produce offspring that are likely to disperse to varying amounts. It is unclear whether this production of larvae with variable dispersal potentials represents a ‘bet-hedging’ strategy (Laaksonen, 2004; Raimondi and Keough, 1990) or is merely a physiological artefact (Eckelbarger, 1986). Nonetheless, it appears marine invertebrates that produce non-feeding larvae have the previously unanticipated potential to control the dispersal of their offspring (Marshall and Keough, 2003c). Interestingly, McGinley *et al.* (1987) state that for a strategy of producing offspring of variable size to be adaptive, mothers must be able to control the dispersal of their offspring into different habitats and this criterion may apply for this group of organisms. Further work is necessary to determine the prevalence of the larval size–swimming time relationship, but we believe a relationship is likely given the demonstrated post-metamorphic cost of extended larval swimming in marine invertebrates with non-feeding larvae (Maldonado and Young, 1999; Marshall *et al.*, 2003b; Wendt, 1998, 2000). If larger larvae have greater nutritional resources, they may be better able to ‘afford’ to delay their metamorphosis until a suitable settlement surface is found. Alternatively, for the ciliated bryozoan larvae at least, larger larvae will have a lower ciliated surface area to volume ratio and thus may expend proportionately less energy than smaller larvae while in the plankton (Wendt, 2000).

3.2.3. Direct developers

As far as we are aware, there is very little information on how offspring size affects developmental time in direct developers. Kohn and Perron (1994) provide an excellent compilation of the literature on *Conus* that show that egg size is strongly related to the length of the pre-hatching period, pooling across indirect and direct developers and this strongly suggests that among these species, larger offspring take longer time to develop. In another example for direct developers, Steer *et al.* (2004) found that manipulating maternal nutrition affected offspring size in the squid *Euprymna tasmanica* and that hatching success was positively correlated with offspring size.

3.2.4. Summary

Table 1.1 summarizes our findings regarding offspring-size effects on the developmental/planktonic period. In general, the apparent lack of a clear effect of egg size on pre-feeding developmental time or the overall planktonic period of planktotrophs was surprising given the number of modelling studies including this as an explicit assumption. Based on the above information, it would appear premature to conclude that increasing egg size results in a decrease in the planktonic period of species with feeding larvae, and further work is needed to establish the relative effects of egg size on the

Table 1.1 Summary of the effects of offspring size on developmental time in planktotrophs and non-feeding larvae

Group	Interspecific	Intraspecific
*Planktotroph*s: pre-feeding period		
Gastropods (*Conus*)	✓ (+ve)	
Copepods		✓ (+ve)
Echinoids	✗	
Opisthobranchs	No data	✗
*Planktotroph*s: planktonic period		
Gastropods (*Conus*)	✓ (−ve)	
Echinoids	✓ (−ve)	Variable
Asteroids	✗	No data
Opisthobranchs	✗	No data
Polychaetes	✗	No data
Lecithotrophs		
Opisthobranchs	No data	✗
Ascidians	✓ (+ve)[a]	✓ (+ve)
Anthozoa	No data	✓ (+ve)
Bryozoa	No data	✓ (+ve)

[a] Developmental time only.

Ticks indicate an effect of offspring size and crosses indicate that no effect was detected.

pre-feeding and feeding periods. In particular, more information on groups other than the echinoids and more intraspecific comparisons are necessary if we hope to understand the crucial relationship between egg size and planktonic period in planktotrophs.

The effects of offspring size on developmental/planktonic period in species with non-feeding larvae appear to be more consistent, but in this group there were also some surprises regarding the settlement behaviour of larvae. Offspring size may not only affect developmental time as previously thought but it also appears to affect larval settlement behaviour (and thus overall planktonic period) in at least two phyla. Together, these data suggest that marine invertebrate mothers may have more 'control' over the dispersal potential of their offspring than previously thought.

3.3. Post-metamorphosis

3.3.1. Planktotrophs

There have been few studies examining the post-metamorphic effects of egg size in planktotrophs. Given that most planktotrophic larvae greatly increase in size from fertilization through to metamorphosis and take in a large amount of exogenous resources through feeding, it is perhaps unsurprising that there has been little interest in post-metamorphic egg size effects in this group. Intuitively, one would expect there to be a weaker link between maternal provisioning and post-metamorphic performance in this group than in other groups where the newly metamorphosed individuals rely entirely on maternal provisioning. However, the lack of studies reduces our confidence in any predictions about the strength of post-metamorphic effects of size in this group. Because no study has examined the effects of offspring size on post-metamorphic performance directly for planktotrophs, here we examine whether egg size affects post-metamorphic/juvenile size. Juvenile size in lecithotrophs and direct developers has strong effects on post-metamorphic performance (see Section 3.3.3) and settler size variation due to larval feeding can have strong effects on the post-metamorphic performance of planktotrophs (Phillips, 2002). Thus, we use post-metamorphic size as a proxy for performance to examine if egg size can affect this parameter in planktotrophs.

Interspecific comparisons of egg size and juvenile size in planktotrophs show variable results. Levitan (2000) found no relationship between egg size and size at metamorphosis among 25 species of echinoids after adjusting for phylogenetic effects. He concluded that it was reasonable to assume that size at metamorphosis was independent of egg size in this group. Similarly, Hadfield and Miller (1987) found no relationship between egg size and settler size among species of opisthobranchs, and Kohn and Perron (1994) found no relationship among species of *Conus*. In contrast, for calyptraeid gastropods there is a positive relationship between egg size and settler size.

Collin (2003) found no relationship overall between egg size and settler size, but we found a significant positive relationship ($R^2 = 0.413$, $n = 10$, $P = 0.045$) in our analysis of Collin's data for just the planktotrophs.

Intraspecific comparisons of egg size effects on post-metamorphic size come exclusively from the echinoids and have also yielded variable results. For the echinoid *A. lixula*, George *et al.* (1990) found strong effects of initial egg size and population source on the size of metamorphosed post-larvae. Post-larvae from large eggs from adults from a favourable site were (mean ± SE) 346 μm (±26.3) in diameter, whereas post-larvae from small egg from adults from a less favourable site were 290 μm (±28.9). However, studies that utilize natural variation in egg size in planktotrophs without the confounding effect of coming from different sites appear to be rare. Most of the remaining comparisons are based on the fairly extreme reduction in offspring size by halving (or quartering) egg size experimentally during development. We have reservations regarding the relevance of this technique for examining the ecological role of natural variation in egg size in planktotrophs, but it does serve to parameterize the potential effects of egg size. Hart (1995) found that experimentally halving the eggs of *S. droebachiensis* resulted in juveniles that were significantly smaller than juveniles from unmanipulated eggs. Although he concluded that the effects were small, the differences in test diameters that he observed resulted in an approximately 15% difference in volume between the two groups and explained the bulk of the variation in juvenile size (Hart, 1995). In contrast, similar experiments on the same species conducted by Sinervo and McEdward (1988) found no effect of egg size manipulation on subsequent juvenile size. Interestingly, Sinervo and McEdward (1988) found an effect of initial egg size on developmental time (halved eggs took longer to develop) whereas Hart (1995) did not. It may be that initial egg size can affect either length of planktonic period or juvenile size even in the same species. Allen *et al.* (2006) demonstrated that manipulating egg size had strong effects on post-settlement size in *Clypeaster rosaceus* and generally, halving egg size had a larger effect than manipulating larval food. It is possible that egg size has more of an effect in planktotrophs with large eggs (*C. rosaceus* is facultatively planktotrophic) than species with small eggs. Alternatively, the different larval food levels could also explain variation in the results of different studies. Regardless, it appears that in some species at least, significant differences in initial egg size can persist through to metamorphosis despite a period of larval feeding and therefore, egg size has the potential to affect post-metamorphic performance in planktotrophs.

3.3.2. Non-feeding larvae

Most of the evidence of post-metamorphic effects of offspring size on post-metamorphic performance comes from species with a non-feeding larval stage. This is probably due to the fact that a number of these studies focus on colonial invertebrates where post-metamorphic survival and growth are easily quantified. The majority of studies examining offspring-size effects for this group involve field studies where larvae are measured in the laboratory, settled onto artificial substrata and then transplanted into the field. However, the effects of larval size on post-metamorphic growth are not restricted to colonial organisms. Emlet and Hoegh-Guldberg's working on the sea urchin *H. erythrogramma* was one of the first studies to show that, in lecithotrophic species, the majority of maternal investment (in their case lipid reserves) was unnecessary for larval development and was probably for post-metamorphic performance (Emlet and Hoegh-Guldberg, 1997). Accordingly, they found that larval lipid reductions did not affect larval performance but had a strong effect on post-metamorphic survival and growth in this species. Ito (1997) also showed that time until starvation in newly metamorphosed 'benthic larvae' of the opisthobranch *Haloa japonica* was positively correlated with initial egg size.

For the bryozoan *Bugula neritina*, larval size affects early post-settlement mortality, early growth, reproduction and the quality of offspring produced in the subsequent generation (Marshall *et al.*, 2003a). The effects of larval size differed between populations for this species: an effect of larval size on survival was detected throughout the life of *B. neritina* colonies in southern Australia, but these effects were more transient in Florida, United States. We suggested that the differential effects of larval size on survival were due to different intensities and sources of mortality between the two sites. At Florida, the principal source of mortality appeared to be detachment during severe storms. While survival was size-dependent initially in Florida, the size-independent mortality associated with storms removed any relationship between larval size and adult survival. In contrast, the only mortality that Australian *B. neritina* experienced was early mortality after settlement, and thus overall mortality was strongly dependent on larval size. This early, size-dependent mortality of sessile invertebrates appears to be relatively common and one of the few generalizations that can be made about the post-metamorphic effects of offspring size. Settlers coming from larger larvae have higher initial survivorship than those from smaller larvae in at least four different taxa (Table 1.2). For non-feeding larvae, the first time an individual is able to feed is once metamorphosis is complete and feeding structures are fully functioning. This is clearly an energetically expensive process and values of 10–60% of total energetic reserves being expended during metamorphosis have been reported (reviewed in Bennett and Marshall, 2005). Given the high energetic cost of metamorphosis, it may be that settlers from smaller larvae are closer to their energetic minimum and if conditions are not ideal (i.e., abundant food available immediately after settlement), then these larvae are more likely to starve to death. Alternatively, settlers from smaller larvae may be unable to exploit food resources as efficiently because they can have smaller feeding structures (Marshall and Keough, 2003a, 2005).

Table 1.2 Summary of studies of post-metamorphic effects of offspring size in marine invertebrates

Study	Location	Species	Size range	Survival	Growth	Reproduction
Marshall *et al.*, 2006	Field	*Botrylloides violaceus*	3-fold	✓ (0–100%)	✓	N/A
Marshall *et al.*, 2003	Field	*Bugula neritina* (Australia)	2-fold	✓ (0–90%)	✓	✓
Marshall *et al.*, 2003	Field	*Bugula neritina* (Florida)		× (early effects only)	✓	N/A
Marshall and Keough, 2003	Field	*Ciona intestinalis*	∼1.2-fold	✓ (22–65%)	N/A	N/A
Marshall and Keough, 2004a	Field	*Watersipora subtorquata* (settlement plates)	2.5-fold	✓ (47–98%)	×	N/A
Marshall and Keough, 2004	Field	*Watersipora subtorquata* (pier pilings)		×	✓	N/A
Marshall and Keough, 2005	Field	*Diplosoma listerianum*		× (early effects only)	× (early effects only)	N/A
Moran and Emlet, 2001	Field	*Nucella ostrina*	∼1.5-fold	✓ (43–62%)[a]	✓	N/A
Rivest, 1983	Lab	*Searlesia dira*		✓	✓	N/A
Emlet and Hoegh-Guldberg, 1997	Lab	*Heliocidaris erythrogramma*		✓	✓	N/A
Ito, 1997	Lab	*Haloa japonica*		✓ (time until starvation)		

[a] Calculated from Figure 4, p. 1604.

Ticks indicate a positive effect of offspring size and crosses indicate that no effect was detected.

Regardless, the effect of larval size on post-metamorphic survival for species with non-feeding larvae (at least for filter feeders) appears to be mediated by nutrition. This is supported by the fact that the effects of larval size on survival in the ascidian *C. intestinalis* are exacerbated at higher settler densities when competition for food is more likely to occur (Marshall and Keough, 2003a). Thus, we predict that when food is more abundant, the effects of larval size on post-metamorphic survival are likely to be reduced.

Initial studies suggest that disturbance as a source of post-settlement mortality acts in a size-independent manner. As described above, colony survival was unrelated to initial larval size in Florida due to storms causing high mortality of *B. neritina* colonies throughout the adult stage. In a study on the encrusting bryozoan *Watersipora subtorquata*, we found that colony survival was dependent on initial larval size for colonies on settlement plates but was independent of larval size for colonies on pier pilings among natural communities (Marshall and Keough, 2004a). Mortality was much higher for colonies on pier pilings, and we suggested that increased mortality through trampling or predation for settlers in this habitat was likely to act in a size-independent way. Overall, we propose that larval size will mediate the nutritional aspects of post-settlement survival but will have little effect on survival if there are high levels of (both biotic and abiotic) disturbance (Brockelman, 1975). Generally, more work is necessary to examine explicitly how biotic factors like predation and competition affect the relationship between larval size and post-settlement survival.

The effects of larval size appear to persist throughout so as to affect subsequent growth in some marine invertebrates with non-feeding larvae. For *B. neritina*, colonies from larger larvae have higher growth rates than colonies from smaller larvae, and these effects can be detected for up to six weeks post-settlement (Marshall *et al.*, 2003). Other sources of variation in larval quality affect *B. neritina* in a similar manner (Wendt, 1998), and it may be that larval quality effects are particularly persistent in this species. For two other species of colonial invertebrate, *Diplosoma listerianum* and *W. subtorquata*, we found initial effects of larval size on colony growth, although these effects were generally less persistent in both species (Marshall and Keough, 2004a, 2005). We speculate that in 'weedy' species, such as *D. listerianum* and *W. subtorquata*, larval-size effects on growth can be quickly obscured due to factors such as the availability of free space and colony fragmentation affecting colony growth. This suggestion is partially supported by the finding that larval-size effects on colony size are far more persistent in the superior competitor *Botrylloides violaceus* (Marshall *et al.*, 2006). The mechanism underlying the effect of larval size on post-metamorphic growth appears to vary between species. For example, in the colonial ascidians *D. listerianum* and *B. violaceus*, larval size positively affects the size of feeding structures (Marshall and Keough, 2005; Marshall *et al.*, 2006). However, larval size can also affect the budding rate of new settlers with settlers from larger larvae budding at higher rates than settlers from smaller larvae (Marshall and Keough, 2004a; Marshall *et al.*, 2006). Given the strong effects of offspring size on growth in colonial invertebrates, it is perhaps unsurprising that offspring size also strongly affects intraspecific competitive interactions. For the colonial ascidian *B. violaceus*, not only were larger larvae more likely to survive and grow faster as colonies than smaller larvae but also they were better competitors (Marshall *et al.*, 2006). When established colonies were present, new recruits from larger larvae were more likely to survive than recruits from smaller larvae, and at higher settler densities the advantages of increased offspring size were exacerbated. Finally, when settlers were placed within proximity to one another, settlers from smaller larvae were more likely to lose territory (without being overgrown) to settlers derived from larger larvae.

The effect of larval size on subsequent reproduction is the most important life-history variable to measure as this parameter gives the most relevant measure of offspring fitness (Stearns, 1992). However, we are aware of only one species for which the effect of larval size on subsequent reproduction has been determined: we found that colonies from larger larvae generally have greater reproduction than colonies from smaller larvae in *B. neritina* (Marshall, 2005; Marshall *et al.*, 2003a). However, these effects vary among different populations, apparently according to local selection pressures. For example, for *B. neritina* colonies that come from populations that are highly seasonal with mortality at the end of the summer, larval size affects the time until reproduction with colonies from larger larvae reproducing before colonies from smaller larvae (Marshall, 2005). In contrast, for colonies where there are high rates of predation but colonies as a whole persist year round, larval size affects growth rates and fecundity much more strongly (Marshall, 2005). Although direct evidence is limited, the strong effects of larval size on post-metamorphic growth suggest that larval size will also affect reproduction in a range of taxa (especially colonial organisms) but more tests are needed.

3.3.3. Direct developers

The direct developers as a group have received less attention with regard to the effects of offspring size on post-metamorphic performance, perhaps because they are mobile as juveniles and therefore harder to track than sessile invertebrates. Despite the challenges involved, Moran and Emlet (2001) examined the effects of offspring size on post-metamorphic performance in the field for an intertidal, direct developing gastropod. After one month in the field, they found that larger hatchlings were more likely to be recovered from the field (the authors inferred greater survivorship from recovery rates) than smaller hatchlings during the winter but during the summer, when survival was lower overall, they found no effect of offspring size on recovery rates. They suggested that desiccation or thermal stress was the main source of mortality (this was supported by the fact that more snails died on the sun-exposed experimental patch than the shaded patch), and that this source of mortality was likely to be independent of offspring size (Moran and Emlet, 2001). Moran and Emlet (2001) also showed that larger hatchlings had higher post-metamorphic growth in the field in all experimental runs. This may be due to the fact that larger hatchlings are more likely to be successful when attacking larger prey items (barnacles; Palmer, 1990). Rivest (1983) found that hatchling size affected post-metamorphic growth rates in the snail *Searlesia dira* with larger hatchlings growing faster. Interestingly, he also found that larger hatchlings were less likely to be successfully preyed upon by the crab *Pagurus hirsutiuculus*, which showed strong preferences for smaller hatchlings. This appears to be the only study to have addressed the effect of offspring size on predation rates in marine invertebrates.

3.3.4. Summary

Offspring size has the potential to affect post-metamorphic survival, growth and even reproduction although evidence is limited by the paucity of studies. Table 1.2 compares the average survivorship of individuals across the size ranges observed for each field study. The effects of size are variable among species with some small differences in size resulting in large differences in survivorship (e.g., *Nucella*) and vice versa (e.g., *Watersipora*). Thus, even small differences in maternal provisioning can result in differential survivorship, and this raises an interesting possibility concerning planktotrophs. Given the range of offspring sizes over which survival differences are observed in lecithotrophs and direct developers, we believe that the degree of variation in settler sizes was induced by egg size in planktotrophs, means that post-metamorphic effects of egg size in the group should not be ruled out.

We propose a number of predictions with regard to offspring-size effects on post-metamorphic performance, all of which should be relatively straightforward to test. First, for species with non-feeding larvae that produce offspring that are at the smaller end of the size spectrum (e.g., most solitary ascidians), we predict that offspring size will affect post-metamorphic survival much more strongly than for those species with extremely large/yolky eggs or larvae that are brooded (e.g., colonial ascidian larvae). In other words, we predict that the *within*-species effects of offspring size will vary *among* species with different mean offspring sizes. Species with smaller eggs are probably closer to their energetic minimum requirements, and less well-provisioned offspring within this group probably require high-food conditions immediately after settlement to survive. In contrast, in species with much larger offspring, larvae are probably further from their energetic minimum requirements and therefore variation in offspring size is likely to affect subsequent growth rates rather than survival. At the very least, we expect that the relationship between offspring size and survival to be more sensitive to variation in food availability in species with relatively smaller eggs as opposed to those with larger eggs.

Second, we predict that different sources of mortality will be more or less likely to act in an offspring size-dependent manner. For example, physical disturbance and stress (e.g., salinity or heat stress) are likely to cause mortality irrespective of offspring size whereas competition and food availability are likely to be size-dependent. The effects of predation on the relationship between offspring size and performance seem less clear: in some instances offspring size will strongly affect predation rates (Palmer, 1990), but other predators, or biological sources of mortality (e.g., bulldosing by limpets of newly settled barnacles), seem less likely to act in a offspring size-dependent manner. Regardless, we strongly believe that a simple division between 'good' and 'bad' environments (Einum and Fleming, 1999; McGinley *et al.*, 1987; Sargent *et al.*, 1987; Stearns, 1992) is uninformative, and generalizations such as larger offspring being better in a bad environments (while useful in some taxa, e.g., Fox, 2000; Fox and Mousseau, 1996) are unlikely to apply to marine invertebrates. Rather than focusing on merely the intensity of the mortality, the source of mortality should also be considered.

Finally, we predict that offspring size will have very different effects on different post-metamorphic traits among different populations (such as those in Marshall, 2005). Traditionally, the effects of offspring size are viewed as being constant among different environments but a genetic component of offspring-size effects clearly exists (Reznick, 1981). Therefore, it is reasonable to expect that offspring size will affect different traits among different populations.

4. SOURCES OF VARIATION IN OFFSPRING SIZE

Offspring size varies within broods (e.g., Marshall *et al.*, 2000), among broods from the same mother (Chester, 1996; Jones *et al.*, 1996), among mothers and among populations (e.g., George, 1994a; George *et al.*, 1990). Here, we review the sources of variation in offspring size at the within- and among-population levels. A huge literature is devoted to various parameters that cause variation in offspring size and to cover them all here would be tedious and uninformative, so we have attempted to highlight some common and major sources of variation.

4.1. Within populations

4.1.1. Stress

A variety of stresses can affect the size of offspring. One of the earliest studies by Bayne *et al.* (1978) showed that salinity, temperature and food availability can all strongly affect the size (mass) of eggs produced by *Mytilus edulis*. More generally, maternal nutrition can have a strong effect on offspring size in a variety of species (Chester, 1996; George, 1995; Meidel *et al.*, 1999; Qian, 1994; Qian and Chia, 1991; Steer *et al.*, 2004), but not in others (Lewis and Choat, 1993). Our own studies have shown that when the bryozoan *B. neritina* suffers a simulated predation event, colonies reduce the size of their offspring (and therefore offspring fitness) dramatically (Marshall and Keough, 2004b). This may be to increase the colony's ability to recover (Marshall and Keough, 2004b). Generally, offspring size is often positively correlated with maternal resource state, but the effects are variable and more work is needed.

Other stresses can also affect offspring size but have received less attention. Gimenez and Anger (2001) found that salinity stress resulted in an increase in egg size for the crab *Chasmagnathus granulate*. Cox and Ward (2002) found strong effects of pollution on the size of larvae produced by *Montipora capitata* with a remarkable 17% decrease in larval volume (assuming spherical larvae) due to exposure to increased ammonium. Studies in terrestrial organisms suggest that pollution could act as a strong selection pressure on offspring size (Hendrickx *et al.*, 2003a,b). It will be interesting to determine the effect that pollution will have on offspring size in other species as this may represent a previously unrecognized mechanism by which pollution can negatively affect marine populations.

4.1.2. Maternal size

Within species across a wide variety of taxa, offspring size is correlated with maternal size (Sakai and Harada, 2001; Stearns, 1992). This correlation can be negative, for example in *Conus marmoreus*, egg size is negatively correlated with maternal size (Kohn and Perron, 1994) and in *B. neritina*, larval size can be positively or negatively correlated with colony size (Marshall, 2005). However, generally, if there is a correlation between offspring and maternal size, it is positive (Table 1.3).Table 1.3 is probably not an accurate representation of reality given that in many cases the absence of a relationship between maternal size and offspring size is unlikely to be reported. Therefore, the percentage of species where no relationship is present is probably dramatically underestimated. Nevertheless, it is clear that within a range of species, larger mothers produce larger offspring. Interestingly, comparisons among species show the opposite pattern, smaller species tend to produce larger offspring than larger species (Emlet *et al.*, 1987). In non-marine species, maternal–offspring size relationships are common and a variety of adaptive explanations have been proposed for the observed correlations. For example, Sakai and Harada (2001) propose that if larger mothers can provision their offspring more efficiently than smaller mothers, then this will result in a correlation between maternal and offspring size. Alternatively, Parker and Begon (1986) predict that if competition between siblings is likely, then larger, more fecund mothers should produce larger offspring to compensate for increased levels of competition. This may apply

Table 1.3 Summary of studies reporting a relationship between maternal size and offspring size in marine invertebrates

Study	Species	Development	Relationship
Dugan *et al.*, 1991	*Emerita analoga*	P	+ve in 8/22 sites
Damiani, 2003	*Pagurus longicarpus*	P	–
Gimenez and Anger, 2001	*Chasmagnathus granulata*	P	+ve
Clarke, 1992	*Ceratoserolis trilobitoides*	B	+ve
Clarke, 1992	*Serolis polita*	B	–
Willows, 1987	*Ligia oceanica*	?	+ve
Oullet and Plante, 2004	*Homarus americanus*	P	+ve
Kim and Hong, 2004	*Palaemon gravieri*	P	–
Dunn and McCabe, 1995	*Gammarus duebeni*	D	+ve
Chaparro *et al.*, 1999	*Crepidula dilatata*	D	+ve
Valentinsson, 2002	*Buccinum undatum*	D	–
Ito, 1997	*Haloa japonica*	L	+ve
Kohn and Perron, 1994	*Conus* spp. (13 sp.)	P	No relationship in 11/12 species but −ve in *C. armoreus*
Steer *et al.*, 2004	*Euprymna tasmanica*	D	–
McCarthy *et al.*, 2003	*Phragmatpoma lapidosa*	P	–
Bridges and Heppell, 1996	*Streblospio benedicti*	L	+ve
Marshall, 2005; Marshall *et al.*, 2003	*Bugula stolonifera*	L	+ve in 2/3 sites, −ve in 1/3
Marshall *et al.*, 2000	*Pyura stolonifera*	L	+ve

Table 1.3 (*continued*)

Study	Species	Development	Relationship
Marshall and Keough, 2003	*Ciona intestinalis*	L	+ve
Marshall and Keough, 2003	*Uniophora granifera*	L	+ve

P, B, L and D indicate planktotrophic, brooding, lecithotrophic and direct development, respectively. '+ve' indicates a positive correlation between maternal size and offspring size and '–' indicates no relationship.

to direct developers, but competition among sibling larvae in planktotrophic species seems unlikely. Hendry *et al.* (2001) suggest that if the maternal phenotype influences the quality of natal environment (e.g., larger mothers having access to the best spawning sites), then a correlation between offspring size and maternal size should be expected. These are all intriguing possibilities, but we currently have insufficient data to determine if any of these models apply to marine invertebrates. Alternatively, the maternal size–offspring size relationship may be non-adaptive and simply be a product of anatomical scaling constraints (Fox and Czesak, 2000). Regardless, it appears in some species, larger mothers produce larger offspring and so not only are larger mothers contributing *more* offspring to the next generation but also they are contributing offspring of the highest quality. This has interesting implications for fisheries and population demographic models because, generally, populations with larger individuals are more likely to supply recruits in populations that contain mostly small individuals (Birkeland and Dayton, 2005).

4.2. Among populations

4.2.1. Habitat quality

Given the effects of maternal nutrition and stress on offspring size, it is perhaps unsurprising that habitat quality also has a strong effect on the size of offspring. However, as with maternal nutrition, the direction of the effects of habitat quality on offspring size is highly variable (George, 1994, 1995; George *et al.*, 1990). Habitat quality can vary due to an almost endless variety of factors but some commonly reported factors include tidal height, water depth (Bertram and Strathmann, 1998) and wave exposure (Etter, 1989). Generally, in poorer quality/more stressful habitats, offspring size is smaller (references above in Section 4.1.1); however, this is not always the case. It is unclear whether these responses are adaptive: the lack of information emphasizes the fact that very few studies have examined the consequences of offspring-size variation in multiple habitats.

4.2.2. Latitudinal clines

Thorson (1935) first suggested that egg size increases from lower to higher latitudes and initial evidence in *Balanus balanoides* supported this idea (Barnes and Barnes, 1965), but it was noted that the trend was inconsistent and appeared to be more related to winter temperatures than latitude per se. Interest in the effects of latitude on offspring size (in crustaceans in particular) has resumed more recently, and for some species, there is a strong latitudinal cline in offspring size (Hadfield, 1989; Hagstrom and Lonning, 1967; Kokita, 2003; Lardies and Castilla, 2001; Lardies and Wehrtmann, 2001; Wagele, 1987; Wehrtmann and Kattner, 1998). Clearly, selection pressures that act on offspring size are likely to predictably change along latitudinal clines, but we are unaware of any study that specifically addresses the relationship between offspring size and performance and how this changes along latitudes. We believe that such studies are warranted given the surprising results from similar studies on seed size (Moles *et al.*, 2004).

5. OFFSPRING-SIZE MODELS

In this section, we review the various models examining offspring size in marine invertebrates, some of the fundamental knowledge gaps that are currently slowing progress and some problems with the traditional approach to modelling offspring size.

Given the astonishing range of offspring sizes exhibited in marine invertebrates, it comes as no surprise that one of the first attempts using models to understand the selection pressures operating on mothers was done with reference to benthic marine invertebrates (Vance, 1973). Vance's classic work used arbitrary units to determine what size offspring maximized maternal fitness (the number of settling larvae) with respect to a number of parameters. While Vance's work was the earliest work on the issue, Smith and Fretwell's (1974) work was probably more influential among the broader community of ecologists. The two models share two basic features: a trade-off between the size and number of offspring and offspring size-fitness function, with these parameters forming the basis of most of the subsequent life-history models of offspring size. We will now examine these basic components of offspring-size models before examining some of the variations on the theme.

5.1. Offspring size-number trade-off

This is the simplest and most conserved feature of offspring-size optimality models, which typically assume that the number of offspring a mother can produce is inversely proportional to the size of their offspring:

$$N = \frac{C}{s}$$

where N is the number of offspring produced, C is the total resources available for reproduction and s the size of offspring.

Typically, this trade-off is presented as an energetic argument: mothers have a limited amount of energy available for reproduction, so any increase in offspring size will result in a concomitant decrease in fecundity. Note that this argument pertains specifically to the *energetic costs* to the mother rather than the *energetic content* of the offspring, a subtle but important difference. Since the early models of Vance and Smith and Fretwell, there has been a significant effort devoted to determining the relative energetic content of large and small offspring among and within species. Across species, there now appears to be reasonable evidence for a relationship between egg size and energetic content in annelids and echinoderms at least (Jaeckle, 1995; McEdward and Miner, 2001; Pernet and Jaeckle, 2004; Wendt, 2000). Within species, the relationship between egg size and energy content is viewed as being more variable.Table 1.4 summarizes those studies that have examined the relationship between egg size and energetic content within marine invertebrate species. McEdward and colleagues have repeatedly suggested that egg size is not a reliable indicator of maternal investment because some regression equations required large differences in egg size to predict a difference in energetic content (McEdward and Carson, 1987; McEdward and Chia, 1991; McEdward and Coulter, 1987; McEdward and Miner, 2001). We would argue that offspring size is probably a reasonable reflection of offspring energetic content for a number of reasons. First, the most common method by which the energetic content of eggs was estimated in many of the studies that found no relationship between offspring size and energy content was the dichromate oxidation technique as modified by McEdward and Coulter (1987). This technique is now viewed as producing unreliable results for a number of reasons (Gosselin and Qian, 1999; Pernet and Jaeckle, 2004), and so the lack of a relationship may be due to methodological problems. Second, the lack of a significant relationship within some species is almost certainly due to a Type II error as a result of a lack of statistical power. The latter seems likely in some studies where only a small number of eggs were examined per species [e.g., McEdward and Chia (1991) used three values for two of the species in their study]. Thus, we believe it is likely that larger offspring have a higher energetic content than

Table 1.4 Summary of studies examining the relationship between offspring size and energetic content

Study	Species	Method	Correlation	*n* of eggs/female	Notes
McEdward and Chia, 1991	*Henricia* sp.	PD	No, $R = 0.37$	18/2	One point highly influential
McEdward and Chia, 1991	*Solaster endeca*	PD	Yes, $R = 0.84$	20/2	Calculated from graph
McEdward and Chia, 1991	*Solaster dawsoni*	PD	Yes, $R = 0.84$	20/2	
McEdward and Chia, 1991	*Mediaster aequalis*	PD	Yes, $R = 0.616$, P value from 1 tailed test significant	10/1	Calculated from graph
McEdward and Chia, 1991	*Pteraster tesselatus*	PD	Yes, $R = 0.9$	20/2	Calculated from graph
McEdward and Coulter, 1987	*Pteraster tesselatus*	PD	No, $R = 0.25$	44/1	
Clarke, 1992	*Chorismus antarticus*	Elemental carbon	Yes, $R = 0.34$	?/111	Square root from % variance explained
Clarke, 1992	*Notocrangon antarticus*	Elemental carbon	Yes, $R = 0.51$	?/29	Square root from % variance explained
Clarke, 1992	*Eulus gaimadrii*	Elemental carbon	Yes, $R = 0.506$	?/99	Square root from % variance explained

PD = Potassium dichromate micro-oxidation technique.

smaller offspring. However, this does not necessarily mean that offspring size perfectly represents energetic content or, more importantly, that larger offspring cost more to produce.

Although we believe that offspring size may be a reasonable indicator of energetic content in marine invertebrates, we suggest that this line of research is somewhat irrelevant to the central issue of whether mothers face a trade-off between the size and number of their offspring. The crucial component of the offspring size-number trade-off is that larger offspring 'cost' more to produce than small offspring. Remarkably, there have been no tests, to our knowledge, that have examined this or that find a trade-off between the size and number of offspring that are produced. As a first step, comparative analyses across species could be useful (e.g., Elgar, 1990) and Kohn and Perron's (1994) comparisons among *Conus* species certainly suggest a trade-off. However, Stearns (1992) highlights the dangers associated with inferring trade-offs from interspecific studies, and empirical measures of the size and number of offspring produced among different individuals of the same species may be more informative. The lack of tests is surprising given that there are some indications that the relative cost of producing large and small offspring could be non-intuitive. For example, the costs of embryo packaging are likely to be non-trivial (for direct developers especially) and may not scale linearly with offspring size (volume). For example, *Conus* species with larger eggs also produce more expensive protective capsules than species with smaller eggs (Kohn and Perron, 1994). Thus, the relative costs of packaging larger offspring will be different than packaging smaller offspring (assuming that one offspring is included per package), resulting in differences in provisioning efficiency between large and small offspring. Finally, Sakai and Harada (2001) have suggested that if offspring are metabolizing resources as they are provisioned (e.g., in brooding species) and the rate at which mothers can provision their offspring is limited, then larger offspring will tend to take longer time to be provisioned and therefore are less efficient to produce.

Overall the energetic costs of producing offspring may not scale with size and caution should be exercised regarding this assumption. It could be argued that the use of size-number trade-offs may still be appropriate because although offspring size and number may not trade off because of energetic constraints, they almost certainly will trade off because of simple space constraints. The brood capacity of mothers to hold eggs or developing offspring is finite if a mother produces more offspring; she may have to produce offspring of smaller size so that they still fit within her reproductive structures. Furthermore, while offspring size may not perfectly represent energetic investment, it does capture some effects of offspring size that would not be represented by energetic content alone. As shown earlier, some offspring-size effects are essentially energetic effects; larger offspring perform better because they have more resources (e.g., resistance to starvation).

However, other effects of offspring size are simply a product of the physical effect of increased size (e.g., increased target size for fertilization, developmental time), and still others are probably composites of the two (larger ciliated larvae may swim for longer because they have more reserves *and* a lower surface area to volume ratio). Therefore, offspring size captures two aspects of subsequent performance that energetic content alone may not, and given the relative ease of measuring offspring size we suggest that it remains a useful proxy. Nevertheless, more work on the energetic costs of producing large and small offspring is clearly necessary to further resolve this issue.

5.2. Offspring size-fitness function

This part of the offspring-size optimality models has received the most attention while it has been revised repeatedly, a common thread remains at its fundamentals (Table 5). Initial attempts at modelling offspring size focused solely on planktonic survival with decreases in offspring size resulting in a longer planktonic period and thus higher overall mortality (Christiansen and Fenchel, 1979; Vance, 1973a,b). However, later attempts also incorporated the effects of offspring size on fertilization rates (Levitan, 1993; Podolsky and Strathmann, 1996), facultative feeding (McEdward, 1997), generation time (Havenhand, 1993) and post-metamorphic effects of offspring size (Marshall *et al.*, 2006). As shown in Table 1.5, most of the models contain a planktonic mortality function and a function linking offspring size to time spent in the plankton with the majority of modifications of Vance's original model occurring at one or both of these functions.

There are some fundamental knowledge gaps that could drastically change the predictions of each of the models and some reproductive modes that are common in marine invertebrates that are completely ignored. For example, although Christiansen and Fenchel (1979) included the effects of size-dependent planktonic mortality in their model, there have been no empirical studies examining whether larger or smaller larvae (of the same species and age) have a greater probability of survival [note that Levitan (2000) includes a similar component in his model]. We have shown that larger larvae are more likely to reject poor settlement surfaces than are smaller larvae, and so are more likely to settle in higher quality habitats (Marshall and Keough, 2003c). Thus, the benefits of increasing offspring size could be much higher than current models would predict. One group that has been mostly ignored in theoretical models is direct developers. Most marine invertebrate models do not explicitly include any phases that are relevant to this major group. More general models have considered how offspring size might be optimally balanced in a group with high levels of maternal protection (packaging).

Table 1.5 Summary of offspring-size optimality models that are most relevant to marine invertebrates

Study	Provisioning	Fertilization	Planktonic period	Post-metamorphic period
Vance, 1973a	×	×	$\Psi = e^{-MT}$	×
Christiansen and Fenchel, 1979	×	×	$\Psi = e^{-M^\star T}$	×
Sargent *et al.*, 1987	×	×	×	$\Psi = EL(S)$
McEdward, 1997	×	×	$\Psi = e^{-MT^\star}$	×
Levitan, 1993	×	$\Psi = 1 - e^{-\alpha S}$	$\Psi = e^{-MT}$	×
Levitan, 2000	×	$\Psi = 1 - e^{-\alpha S}$	$\Psi = e^{-MT^{\star\star}}$	×
Marshall *et al.*, 2006	×	×	×	$\Psi = L(S)$

Note that the models have been greatly simplified so that their essential structures can be compared. In all of the models, M denotes planktonic mortality rate, T denotes time spent in the plankton and S denotes offspring size. A cross indicates that the model does not include this life-history stage. Ψ represents offspring fitness. E represents pre-hatching survival: e^{-mS}, where m = mortality rate while in the egg; $L(S)$ represents post-metamorphic performance and is a function of S; $T = \lambda + \rho$ where $\lambda = S\beta$ and $\rho = \alpha(1 - S)$, where β and α are constants; $M^\star = P + FS$ where P is mortality common to all sizes and F is a larval size-specific mortality rate; $T^\star = DS + D(1 - S)/F$ where D = time taken to develop at the maximum rate and F = food availability; $T^{\star\star} = S_{\text{fp}}/(S - 1) + T_{\text{fp}}$ where S_{fp} = minimum size where planktonic feeding is unnecessary and T_{fp} = a minimum time in the plankton when feeding does not occur. Note: this assumes that there is no effect of egg size on the pre-feeding period.

The model of Sargent *et al.* (1987) is relevant to encapsulated direct developers: this model assumes that maternal care (packaging) increases offspring survival, larger juveniles have greater performance and larger offspring have longer periods until hatching. Overall, this model predicts that for species with greater levels of maternal care, larger offspring sizes should be favoured (Sargent *et al.*, 1987). For marine direct developers, there is good evidence for each of these assumptions (Kohn and Perron, 1994; Moran and Emlet, 2001; Strathmann, 1995; Strathmann and Chaffee, 1984; Strathmann *et al.*, 2002). We suggest that this model could be applied to direct developers successfully as a way of modelling offspring-size evolution in this group. However, this assumes that the costs of egg packaging can reliably be estimated.

5.3. Reconciling within-clutch variation

All offspring-size optimality models predict at least two stable optima, a 'large offspring-size optimum' where fitness benefits exceed fecundity costs and a 'small offspring-size optimum' where producing infinitely small offspring yields an infinite fecundity (Vance, 1973a,b). The latter optimum is clearly non-sensical and is simply a product of the functions that are used rather than an accurate reflection of biology. Thus, if we ignore optima based on unfeasibly small offspring, in a constant environment, we should expect a single optimum size. Models incorporating the effects of maternal phenotype on the natal environment have become more common (Hendry *et al.*, 2001; Parker and Begon, 1986; Sakai and Harada, 2001). For example, Sakai and Harada (2001) predict that if larger mothers can provision their offspring more efficiently than smaller mothers, then maternal size and offspring size should be correlated. Further, in species of fish where the maternal phenotype has the potential to affect the offspring size–fitness relationship, offspring-size variation within populations is higher (Einum and Fleming, 2004a). These models predict the observed variation in offspring sizes among different mothers and initial empirical evidence is supportive (see Section 4.1.2). While a substantial theory base can now account for variation in offspring size among mothers, explaining the variation in offspring sizes from the same mother has been more problematic. While there are numerous verbal arguments for producing a brood of offspring that vary in size (e.g., Capinera, 1979; Crump, 1981; Dziminski and Roberts, 2005; Lips, 2001), the few theoretical considerations of intra-brood offspring-size variation struggle to find an adaptive basis for this variation (e.g., Einum and Fleming, 2004b; McGinley *et al.*, 1987). In most instances, producing offspring of identical size has the greatest advantage or if producing variable offspring is advantageous, it is only under restrictive and unlikely assumptions. For example, McGinley *et al.* (1987) found that producing offspring of variable size was advantageous only when mothers could strictly control the dispersal of their offspring into the appropriate habitat. Rather than having an adaptive basis, intra-brood variation is increasingly viewed as a product of physiological or genetic constraints that prevent mothers from producing offspring of identical size (Einum and Fleming, 2004b; Fox and Czesak, 2000). In their review of offspring-size effects on insects, Fox and Czesak (2000; p. 358) concluded that '. . . some authors have suggested that at least some of the variation within families is an adaptive response to living in a variable environment. At this time however, there are few experimental studies and too little theoretical work to generalize'. Therefore, despite the intuitive appeal of intra-clutch variation in offspring size as a mechanism for coping with environmental heterogeneity, theoretical evidence for the concept remains elusive. We suggest that the ubiquitous variation in offspring size seen within clutches does not solely occur due to constraints on producing offspring of uniform size and may yet have an adaptive explanation. We believe that the lack of theoretical evidence for adaptive within-clutch variation reflects the modelling approaches that have traditionally been used; optimality models, by definition, predict a single offspring size to maximize fitness (ignoring the nonsensical, minimum optimum). Alternative approaches such as game theoretic models (Geritz, 1995; Geritz *et al.*, 1999) may provide better tools for exploring adaptive variation in offspring size within clutches whereas more traditional, optimality models may still be useful for exploring variation among mothers, populations and species.

5.4. Summary of offspring-size models

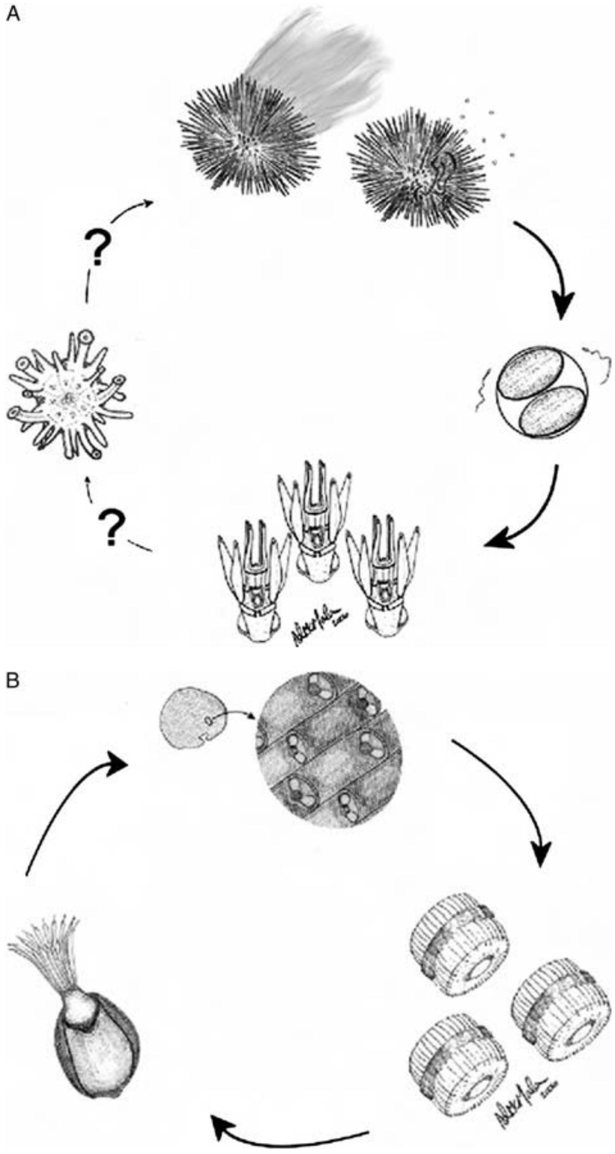
One point this chapter has hopefully made clear is that variation in offspring size can have effects on performance in every life-history stage. Accordingly, theoretical models need to reflect the pervasive nature of offspring-size effects across life-history stages. Ideally, a realistic optimality model should contain the influence of maternal nutritional state, and the relationships between offspring size and fertilization success, planktonic survival, settlement choice and post-metamorphic performance. Once this model has been constructed, then perturbations of the environment in each of these conditions and the relative importance of each life-history stage can be assessed. We suggest that this is where the real value of optimality modelling lies, that is, as tools for examining the relative contribution of each life-history stage to the selective pressures acting on offspring size and for making predictions about how the variation in environmental conditions will influence optimal offspring size. In contrast, these models have been used inappropriately to explain interspecific patterns in offspring-size distributions (e.g., Sewell and Young, 1997; Vance, 1973a,b), and a great deal of effort has been expended to try and match optimality model predictions with the observed distribution of offspring sizes among species (McEdward and Miner, 2006). Such comparisons are inappropriate given that, depending on the relationship between offspring and performance (which of course will vary greatly among species), a very different optimal offspring size will be predicted for each individual species.

6. SUMMARY

Figure 1.7A–C summarize our view of the effects of maternal nutrition on each of the life-history stages for the three broad developmental modes, highlighting the major unknowns for each group and stage. Size of arrow represents our view of the relative strength of offspring-size effects between each stage. The relative strengths also vary with developmental mode.

6.1. Planktotrophs

Despite maternal nutrition constituting a lesser proportion of total larval nutrition in planktotrophs than in other developmental modes, there are strong effects of offspring size on multiple life-history stages of



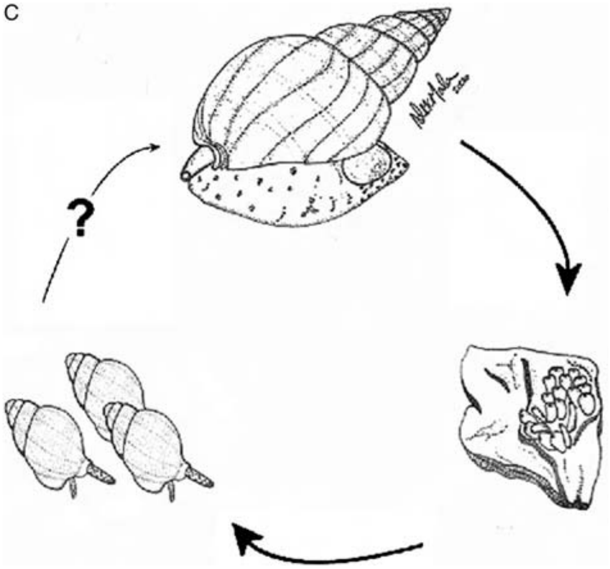


Figure 1.7 Summaries of the effects of offspring size on the various life-history stages of (A) a 'typical' planktotrophic species with external fertilization, (B) a 'typical' lecithotrophic species with internal fertilization and (C) a 'typical' species with direct development. Arrows indicate that we believe there is strong effect of offspring size on that particular life-history stage and question marks indicate that the effects at this stage have not been examined.

planktotrophs. Egg size has strong effects on fertilization in free-spawning species; larger eggs are more likely to be contacted by sperm than smaller eggs (although this may be mitigated by egg accessory features). In many taxa, larvae from larger eggs also spend less time in the plankton than smaller eggs because they appear to require fewer resources before reaching metamorphic competence, although this finding is not universal and more tests are necessary, particularly at the intraspecific level and on 'non-echinoids'. There may be synergistic effects between larvae from larger eggs having greater feeding capacities and more initial resources. The most likely mechanism is increased feeding capacity in larger larvae, leading to higher growth rates. However, there are currently so few data on intraspecific effects of egg size that it is difficult to generalize. Similarly, there are too few data to make definitive conclusions about post-metamorphic effects in planktotrophs but we suggest that post-metamorphic effects cannot be ruled out, because several inter- and intraspecific studies indicate that larger eggs do become larger settlers. Thus, despite its intuitive appeal, the notion that exogenous, larval nutrition overrides any effect of maternal provisioning may be incorrect for planktotrophs.

6.2. Non-feeding

Perhaps unsurprisingly, this group shows the strongest effects of offspring size. Egg size affects fertilization success, developmental time before metamorphic competency in some groups, larval settlement behaviour, maximum larval life span and all elements of post-metamorphic performance, including reproduction and offspring provisioning in the subsequent generation. However, most of the examples come from our own work on colonial invertebrates, and more work on unitary species is necessary to determine the generality of the patterns of offspring-size effects in this group. Non-feeding taxa as a whole are of particular interest because, presumably, larval size affects post-metamorphic performance because of differing levels of larval energetic reserves at metamorphosis. Because larvae do not feed in this group and extended swimming has post-metamorphic consequences (Marshall *et al.*, 2003b; Pechenik *et al.*, 1998), an interesting trade-off exists with regard to whether larger larvae should ‘use’ their extra resources for swimming and maximize their chances of encountering an optimal habitat, or for settling immediately and utilizing these extra resources for enhanced juvenile/adult performance. It would be interesting to determine the relative impact of larval swimming and larval size on post-metamorphic performance and how these two larval nutrition factors interact.

6.3. Direct developers

We suspect that offspring size–performance relationships in the field are likely to be strongest and most consistent in direct developers because there is no larval stage that can affect (through either extended swimming or larval feeding) the relationship between juvenile energy reserves and original maternal provisioning. This is also the group where the highest level of within-population variation in offspring size was observed across species. Interestingly, numerous different pathways for increasing per offspring maternal investment have evolved in species with this developmental mode, including intragonadal sibling cannibalism (Byrne, 2006), nurse eggs (Spight, 1976) and even partial predation on maternal body parts (Emlet, personal communication). Some reproductive strategies will result in mothers having more ‘control’ over the provisioning of offspring than others, for example nurse eggs versus cannibalism. We would expect mothers with more control of the provisioning of their individual offspring to be more likely to be able to adaptively adjust the size of their offspring according to local conditions. Given that direct developers tend to disperse less than other groups and the post-metamorphic effects of offspring size can be so strong in this group, we suggest that local population dynamics are particularly susceptible to variation in offspring quality in this group but this requires testing.

6.4. Ecological implications

What are the consequences of offspring-size variation for recruitment and subsequent population dynamics? Consider a broadcast spawning marine invertebrate with short-lived, lecithotrophic larvae. Clearly, offspring size will affect the number of eggs that are produced, the percentage of eggs that are fertilized, the time that the larvae spend in the plankton, the microhabitats in which the larvae settle and the number of those settled larvae that will survive to reproduction. Hence, offspring-size variation can be viewed to act as a 'filter' on the number of individuals that pass through each stage. If offspring sizes are relatively large, then (all else being equal) more of the eggs will become successful recruits than if offspring sizes are relatively smaller. In other words, the strength of the link between adult reproductive output and subsequent recruitment will be strongly mediated by offspring size. Furthermore, the strength of links among populations will be strongly affected by offspring-size variation through two mechanisms: first, by affecting the dispersal potential of offspring and second, by affecting the chances of those offspring surviving in the new habitat. Offspring-size effects also change the way in which we view source and sink populations; a population that produces very few, large (high quality) offspring may actually contribute more to the recruitment pool than a population that produces many, low quality offspring. It is particularly interesting that maternal phenotype or habitat quality can strongly affect the size of offspring that are produced, suggesting recruitment is coupled not only to offspring quality and quantity but also to broodstock quality.

6.5. Evolutionary implications

In this chapter, we have found strong evidence for offspring size affecting multiple life-history stages. For species with planktonic larvae, this comprises at least three life-history stages (gamete, larvae and juvenile) and three different habitats (maternal habitat, plankton and juvenile habitat) that can be widely separated in space and time. Consequently, it presents a remarkable challenge to marine invertebrate mothers to optimally provision their offspring, especially since there could be conflicting selection pressures on offspring size at each life-history stage. For example, an adult *C. intestinalis* could be at very high densities and so during spawning, its eggs could be more likely to suffer polyspermy, thereby selecting for smaller eggs. However, smaller eggs are less likely to disperse from this high-competition environment, and less likely to perform well under a higher competitive regime than larger eggs (Marshall and Keough, 2003a,b). The way in which marine invertebrate mothers balance these selection pressures and which life-history stage gets 'priority' as a selection pressure remains an intriguing unknown. In other organisms, offspring size is regarded as a highly plastic, adaptive maternal effect (Fox and Czesak, 2000; Fox *et al.*, 1997). Given the complex 'web of selection' acting on marine invertebrate mothers, it will be interesting to determine whether mothers can adaptively adjust the size of their offspring according to local environmental conditions. Our review indicates that direct developers as the most appropriate group for the first examination of this issue as the offspring are less dispersive, and there are few life-history stages in which offspring size can affect performance.

The strong offspring-size effects on fertilization and subsequent performance also have some interesting implications for sexual selection in broadcast spawners. First, it seems that in this group, males will determine the ultimate size of offspring while females determine the range of sizes that can be fertilized. This is because males can control the sperm environment in which eggs are fertilized and ultimately zygote size due to size-dependent fertilization effects (Marshall *et al.*, 2002). Thus, there is the potential for sexual conflict, with females getting the greatest fitness benefits from all of their eggs being fertilized whereas males may get greater benefits if they only release small amounts of sperm, 'prudently' fertilizing only the largest eggs that will have the greatest performance (for discussion of 'prudent' males with regards to sperm release see Wedell *et al.*, 2002). Egg size-dependent fertilization and performance also has some consequences for males: if a male accesses eggs after they have been exposed to another male, then he can only fertilize the 'left over' eggs, which may be eggs that were smaller and less likely to be fertilized by the first male. Therefore, by accessing eggs second, a male suffers two fitness costs: fertilization of fewer eggs (because the remaining eggs are smaller and harder to 'hit') and siring offspring that will have lower performance (Marshall *et al.*, 2004a). Consequently, males will be under strong sexual selection pressure to access a female's brood before any other males.

6.6. Future research directions

The study of post-metamorphic effects of offspring size in marine invertebrates has only just begun and so more work generally is needed. However, we feel there are some priority areas that require addressing. The most commonly cited mechanism for the advantage of increased offspring size is nutritional: larger larvae are more resistant to starvation as settlers than settlers from smaller larvae. There is currently little direct evidence to support this hypothesis. Simple experiments examining the relative importance of offspring size under high- and low-food regimes could address this important gap in our knowledge. Apart from preliminary laboratory studies, there are few studies examining how offspring size affects predation rates. Plant ecologists have been addressing the analogous problem in plants for many years and have used caging studies to examine the interaction between herbivory and optimal seed size (Stanton, 1984, 1985). These experiments could be easily transferred to sessile invertebrates. The final priority area that we feel requires urgent attention is examination of offspring-size effects in more diverse habitats. Thus far, post-metamorphic offspring-size effects in marine invertebrates have focused entirely upon temperate, hard substrate environments (benthic subtidal and rocky intertidal), whereas soft sediment environments (intertidal and subtidal) and coral reefs have received no attention whatsoever. Clearly, this important gap in our understanding of offspring-size effects requires addressing and especially given that offspring sizes show similarly high levels of variation for organisms in these environments when compared to those that have been better studied.

Throughout the discussion of post-metamorphic offspring-size effects, we have emphasized that among different environments or conditions, the effects of offspring size are highly variable. This is a crucial point because ultimately, for any particular species the goal is to determine the relative importance of offspring size. Focusing on any single set of conditions will have limited applicability. Given that the effects of offspring size are so sensitive to local conditions, we believe any study examining offspring-size effects should (1) examine offspring-size effects under as realistic conditions as possible and (2) examine how these effects vary across a range of ecologically relevant stresses. While laboratory studies are essential for the initial establishment of any offspring-size effects (particularly for mobile species), the importance of these effects cannot be estimated until they have been examined in a field context. Numerous studies have shown that laboratory examinations of offspring size will produce misleading conclusions about the strengths of these effects (e.g., Einum and Fleming, 1999; Fox, 2000). We also suggest that further studies on offspring size be conducted at multiple sites with offspring from several populations. By doing so, two issues can be addressed simultaneously. First, the generality of the offspring-size effects can be determined and second, by using several populations, one avoids the potentially erroneous assumption that there is no population-level variation in the relationship between offspring size and performance (Marshall, 2005). Finally, the effects of offspring size should be examined over as much of an organism's life history as possible so as to gather more accurate measures of fitness. Obviously the above suggestions greatly increase the workload of anyone wishing to examine offspring-size effects and, as an example, thus far our own studies have neglected to include all of the above components. However, we believe strongly that the sensitivity of offspring-size effects and their apparent variability among populations lead a risk of highly over- or underestimating the effects of offspring size.

To date, offspring-size effect studies have largely been limited to one or two populations but, given the effects of offspring size on post-metamorphic survival, and the levels of among-population variation in offspring size, it would be interesting to determine whether offspring-size effects 'scale up' to the level of populations. For example, do 'source' populations produce offspring of increased size relative to 'sink' populations. Of particular interest is the examination of how maternal stresses at the level of populations (such as anthropogenic factors like pollution and nutrient enrichment) affect maternal provisioning. In terrestrial systems, it is becoming clear that like many other traits, offspring size is under novel selection pressure from human influences (Hendrickx *et al.*, 2003a,b). Given the likely consequences of offspring-size variation for recruitment in marine invertebrates and the initial strong effects of pollutants on maternal provisioning (Cox and Ward, 2002), there may be strong underlying impacts of pollutants that are going undetected.

With regard to the next steps in theoretical studies, we suggest the need for more integrative models that take the effects of offspring size on every life-history stage into account, from the production of gametes through to reproductive maturity of the offspring. Models that examine the influence of recruit quality and its consequences for population connectivity would also greatly enhance our ability to determine the relative importance of larval quality and quantity.

APPENDIX

Variation in offspring size in marine invertebrates with direct (D), lecithotrophic (L) and planktotrophic (P) development and internal (I) or external (E) fertilization. Offspring sizes are given as diameters and CVs are calculated as total variation.

Phylum, Class	Order	Family	Species	Study	Development	Fertilization	Eggs/ mother	Number of mothers	Offspring size	CV
Cnidaria, Anthozoa	Scleractinia	Acroporidae	*Acropora spathulata*	Baird *et al.*, 2001	L	E	32	6–8	557	9.33
	Scleractinia	Acroporidae	*Acropora hyacinthus*	Baird *et al.*, 2001	L	E	18	6–8	553	4.70
	Scleractinia	Acroporidae	*Acropora millepora*	Baird *et al.*, 2001	L	E	32	6–8	541	5.91
	Scleractinia	Acroporidae	*Astreopora myriophthalma*	Baird *et al.*, 2001	L	E	49	6–8	538	3.38
	Scleractinia	Faviidae	*Favites halicora*	Baird *et al.*, 2001	L	E	20	6–8	401	8.72
	Scleractinia	Faviidae	*Goniastrea retiformis*	Baird *et al.*, 2001	L	E	38	6–8	371	5.66
	Scleractinia	Agariciidae	*Pachyseris speciosa*	Baird *et al.*, 2001	L	E	30	6–8	368	5.16
	Scleractinia	Acroporidae	*Montipora digitata*	Baird *et al.*, 2001	L	E	39	6–8	337	12.16
	Scleractinia	Pocillporidae	*Pocillopora damicornis*	Harii *et al.*, 2002	L	I	20	5	1000	20
	Helioporacea	Helioporidae	*Heliopora coerulea*	Harii *et al.*, 2002	L	I	25	10	3700	10.81
Cnidaria, Hydrozoa	Hydroida	Tubulariidae	*Tubularia mesenbryanthemum*	Yamashita *et al.*, 2003	L	I	30	10	305	10.88
Platyhelminthes, Turbellaria	Polycladida	Stylochidae	*Stylochus ellipticus*	Chintala and Kennedy, 1993	P	I	50	?	68.5	4.52
Annellida, Polycheata	Sabellida	Serpulidae	*Hydroides dianthus*	Toonen and Pawlik, 2001	P	E	?	15	60.7	8.23
	Sabellida	Spirorbidae	*Bushiella abnormis*	Hess, 1993	L	I	?	9	185	21.62
	Sabellida	Spirorbidae	*Circeis armoricana*	Hess, 1993	L	I	?	11	167	10.17
	Sabellida	Spirorbidae	*Paradexiospira vitrea*	Hess, 1993	L	I	?	11	196	9.18
	Sabellida	Spirorbidae	*Pileolaria berkelyana*	Hess, 1993	L	I	?	5	169	7.69
	Sabellida	Spirorbidae	*Protolaeospira exima*	Hess, 1993	L	I	?	7	199	10.55
	Terebellida	Sabellariidae	*Phragmatopoma lapidosa*	McCarthy *et al.*, 2003	P	E	?	20	90.4	4.09
Mollusca, Bivalvia	Pteroida	Pectinidae	*Chlamys bifrons*	Styan and Butler, 2000	P	E	10	8	116.5	2.66
	Pteroida	Pectinidae	*Chlamys asperrima*	Styan and Butler, 2000	P	E	10	6	71.2	5.67
	Mytiloida	Mytilidae	*Brachidontes virgiliae*	Bernard *et al.*, 1988	L	I	300	?	383	13.31
	Veneroida	Tellinidae	*Macoma mitchelli*	Kennedy and Lutz, 1989	P	E	25	?	59	3.89
	Ostreina	Ostreidae	*Ostrea edulis*	Jonsson *et al.*, 1999	P	I	40	120	202	5.94
	Veneroida	Tridacnidae	*Tridacna squamosa*	Fitt and Trench, 1981	P	E	10	?	158	4.43
Mollusca, Gastropoda	Archaeogastropoda	Trochidae	*Cantharidus callichroa*	Ho Sun and Hong, 1994	L	I	30	?	446	10.76
	Neogastropoda	Buccinidae	*Engoniophos unicinctus*	Miloslavich and Penchazadeh, 1994	D		?	49	1007.5	25.60
	Neogastropoda	Columbellidae	*Strombina francesae*	Cipriani and Penchazadeh, 1993	D		20	1	571	6.12
	Neogastropoda	Columbellidae	*Strombina pumilio*	Cipriani and Penchazadeh, 1993	D		11	?	947	10.24
	Mesogastropoda	Cypraeidae	*Cypraea caputdraconis*	Osorio *et al.*, 1992	P	I	125	11	112	5.1
	Mesogastropoda	Strombidae	*Strombus gigas*	Davis *et al.*, 1993	P	I	20	3	225	7.56
	Mesogastropoda	Strombidae	*Strombus costatus*	Davis *et al.*, 1993	P	I	30	3	262	2.29
	Mesogastropoda	Strombidae	*Strombus raninus*	Davis *et al.*, 1993	P	I	20	9	140	2.85
	Neogastropoda	Muricidae	*Drupella cornus*	Turner, 1992	P	I	200	7	170	1.47
	Mesogastropoda	Vermetidae	*Vermetus* sp.	Miloslavich and Penchazadeh, 1992	L	I	33	49	240	5.83
	Mesogastropoda	Vermetidae	*Dendropoma corrodens*	Miloslavich and Penchazadeh, 1992	D		134	27	512	11.52

(*continued*)

Appendix (*continued*)

Phylum, Class	Order	Family	Species	Study	Development	Fertilization	Eggs/ mother	Number of mothers	Offspring size	CV
	Mesogastropoda	Cassidae	*Cypraecassis testiculus*	Hughes and Hughes, 1987	P	I	28	2	149	10.06
	Mesogastropoda	Vermetidae	*Petaloconchus montereyensis*	Hadfield, 1989	D		74	16	1450	5.51
	Neogastropoda	Buccinidae	*Babylonia areolata*	Chaitanawisuti and Kritsanapuntu, 1997	P	I	?	35	425.7	5.40
	Neogastropoda	Buccinidae	*Searlesia dira*	Rivest, 1983	D		?	?	1490	18.12
	Neogastropoda	Muricidae	*Nucella crassilabrum*	Gallardo, 1979	D		?	?	1131	8.71
	Neogastropoda	Muricidae	*Thais emarginata*	Spight, 1976	D		?	?	1330	13.23
	Neogastropoda	Muricidae	*Acanthina spirata*	Spight, 1976	D		?	?	671	8.64
	Mesogastropoda	Vermetidae	*Dendropoma petraeum*	Calvo *et al.*, 1998	D		40	?	756	10.73
	Mesogastropoda	Naticidae	*Polinices lewisii*	Pedersen and Page, 2000	P	I	5	?	235.4	2.33
	Mesogastropoda	Calyptraeidae	*Crepidula adunca*	Collin, 2000	D		?	?	2200	25.71
	Neogastropoda	Muricidae	*Nucella lapillus*	Etter, 1989	D		40	5	1270	14.40
	Stylommatophora	Odostomiidae	*Odostomia columbiana*	Collin and Wise, 1997	P	I	??	23?	74	2.17
	Mesogastropoda	Calyptraeidae	*Crucibulum quirqinae*	Veliz *et al.*, 2001	P	I	309	14	325.8	6.59
	Mesogastropoda	Calyptraeidae	*Crucibulum quirqinae*	Veliz *et al.*, 2001	D		69	18	720	17.12
	Neogastropoda	Buccinidae	*Buccinum cyaneum*	Miloslavich and Dufresne, 1994	D		204	33?	1520	19.078
	Mesogastropoda	Calyptraeidae	*Crepidula dilatata*	Gallardo, 1977	P	I	?	?	218	3.66
	Mesogastropoda	Calyptraeidae	*Crepidula dilatata*	Gallardo, 1977	D		?	?	234	7.86
	Archaeogastropoda	Trochidae	*Calliostoma zizyphinum*	Holmes, 1997	L	E	100	9	300	3.12
	Mesogastropoda	Cymatiidae	*Cymatium cutaceum*	Ramon, 1991	P	I	15	1	151	5.03
	Mesogastropoda	Cymatiidae	*Cymatium corrugatum*	Ramon, 1991	P	I	15	1	216	3.425
Mollusca, Opisthobranchia	Cephalaspidea	Atyidae	*Haminoea vesicula*	Gibson and Chia, 1989	P	I	15	30	90	3.33
	Nudibranchia	Doridae	*Aldaria proxima*	Jones *et al.*, 1996	P	I	12	18	168	4.57
	Cephalaspidea	Bullidae	*Bulla gouldiana*	Farfan and Ramirez, 1988	P	I	?	15–30	84.5	4.52
Mollusca, Celphalopoda	Teuthida	Loliginidae	*Sepioteuthis australis*	Steer *et al.*, 2003	D	?	?	5	4800	13.12
Crustacea, Malacostraca	Decapoda	Geryonidae	*Geryon (Chaceon) fenneri*	Hines, 1988	P	I	?	12	567	2.64
	Decapoda	Geryonidae	*Geryon (Chaceon) quinquedens*	Hines, 1988	P	I	?	17	731	3.83
	Decapoda	Paguridae	*Pagurus longicarpus*	Damiani, 2003	P	I	?	49	410	6.09
Crustacea, Copepoda	Harpacticoida	Harpacticidae	*Euterpina acutifrons*	Guisande *et al.*, 1996	P	I	290–497	20	62.4	0.70
Crustacea, Maxillopoda	Thoracia	Balanidae	*Balanus balanoides*	Barnes and Barnes, 1965	P	I	?	?	283	4.94
	Thoracia	Verrucidae	*Verruca stroemia*	Barnes, 1953	P	I	?	?	565	5.3
	Thoracia	Chamalidae	*Chthamalus dentatus*	Achituv and Wortzlavski, 1983	P	I	?	16	190.9	4.6
	Thoracia	Chthamalidae	*Octomeris angulosa*	Achituv and Wortzlavski, 1983	P	I	?	10	211.7	3.77

Bryozoa, Gymnolaemata	Cheilostomata	Bugulidae	*Bugula stolonifera*	Wendt, 2000	L	I	?	?	160	7.90
	Cheilostomata	Bugulidae	*Bugula simplex*	Wendt, 2000	L	I	?	?	207	19.43
	Cheilostomata	Bugulidae	*Bugula turrita*	Wendt, 2000	L	I	?	?	202	6.64
	Cheilostomata	Bugulidae	*Bugula neritina*	Marshall *et al.*, 2003	L	I	?	?	271	6.90
	Cheilostomata	Watersiporidae	*Watersipora subtorquata*	Marshall and Keough, 2004	L	I	?	?	323.18	11
Echinodermata, Echinoida	Clypeasteroida	Dendrasteridae	*Dendraster excentricus*	Podolsky, 2002	P	E	10	6	129	3.5
	Arbacioida	Arbaciidae	*Arbacia lixula*	George *et al.*, 1990	P	E	100	10	76.6	4.30
	Cidaroida	Cidaridae	*Phyllacanthus imperialis*	Olson *et al.*, 1993	L	E	10	20	507	6.29
	Clypeasteroida	Clypeasteridae	*Clypeaster rosaceus*	Emlet, 1986	FP	E	25	?	280.3	2.74
	Clypeasteroida	Clypeasteridae	*Clypeaster subdepressus*	Emlet, 1986	P	E	25	?	152.6	2.29
Echinodermata, Asteroida	Platyasterida	Luidiidae	*Luidia maculata*	Komatsu *et al.*, 1994	P	E	?	?	173	3.46
	Platyasterida	Luidiidae	*Luidia foliolata*	George, 1994	P	E	20	1	144.3	4.78
	Spinulosida	Echinoasteridae	*Echinaster* morph 1	Scheibling and Lawrence, 1982	L	E	9	10 × 12 × 3	840	4.76
	Spinulosida	Echinoasteridae	*Echinaster* morph 2	Scheibling and Lawrence, 1982	D	E	12	10 × 12 × 3	960	5.2
	Platyasterida	Luidiidae	*Luidia quinaria*	Komatsu *et al.*, 1982	P	E	60	?	124	4.91
	Paxillosida	Astropectentidae	*Astropecten gisselbrechti*	Komatsu and Nojima, 1985	L	E	17	?	353	5.09
	Forcipulata	Asteriidae	*Pisaster brevispinus*	Fraser *et al.*, 1981	P	E	?	?	165	3.33
	Forcipulata	Asteriidae	*Pisaster ochraceus*	Fraser *et al.*, 1981	P	E	30	5	163	3.68
	Spinulosida	Poraniidae	*Porania antarctica*	Bosch, 1989	P	E	30	4	548	9.23
	Spinulosida	Poraniidae	*Porania* sp.	Bosch, 1989	L	E	35	7	554	17.08
	Spinulosida	Pterasteridae	*Pteraster militaris*	McClary and Mladenov, 1990	D		?	75	2171	25.10
	Forcipulata	Asteriidae	*Diplasterias brucei*	Bosch and Pearse, 1990	D		105	1	3000	20
	Spinulosida	Asterinidae	*Patiriella regularis*	Byrne, 1991	P	E	10	~10	197	1.92
	Spinulosida	Asterinidae	*Asterina minor*	Komatsu *et al.*, 1979	L	E	37	?	437	6.86
Echinodermata, Ophiuroida	Phrynophiurida	Asteroschematidae	*Astrobrachion constrictum*	Stewart and Mladenov, 1994	L	E	400	16	415	13.49
Echinordermata, Holothuroida	Dendrochirotida	Psolidae	*Psolus chitonoides*	McEuen and Chia, 1991	L	E	10	5	627	5.58
	Dendrochirotida	Psolidae	*Psolidium bullatum*	McEuen and Chia, 1991	L	E	10	2	330	5.15
	Aspidochirotida	Holothuriidae	*Holothuria scabra*	Ramfafia *et al.*, 2000	P	E	?	?	157	2.27
	Apodida	Synaptidae	*Leptosynapta clarki*	Sewell, 1994	D		100	6	2000	52
Chordata, Ascidia	Stolidobranchia	Pyuridae	*Pyura stolonifera*		L	E	100	34	269	9.18
	Aplousobranchia	Didemnidae	*Diplosoma listerianum*		L	I	10	12	976	9.32
	Phlebobranchia	Cionidae	*Ciona intestinalis*		L	E	100	20	145	5.17
	Stolidobranchia	Pyuridae	*Pyura fissa*		L	E	50	10	175.7832	5.21
	Stolidobranchia	Styelidae	*Styela plicata*		L	E	50	10	163	7.9

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AN EVALUATION OF THE EFFECTS OF CONSERVATION AND FISHERY ENHANCEMENT HATCHERIES ON WILD POPULATIONS OF SALMON[1]

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Abstract

The historical, political and scientific aspects of salmon hatchery programmes designed to enhance fishery production, or to recover endangered populations, are reviewed. We start by pointing out that the establishment of hatcheries has been a political response to societal demands for harvest and conservation; given this social context, we then critically examined the levels of activity, the biological risks, and the economic analysis associated with salmon hatchery programmes. A rigorous analysis of the impacts of hatchery programmes was hindered by the lack of standardized data on release sizes and survival rates at all ecological scales, and since hatchery programme objectives are rarely defined, it was also difficult to measure their effectiveness at meeting release objectives. Debates on the genetic effects of hatchery programmes on wild fish have been dominated by whether correct management practices can reduce negative outcomes, but we noted that there has been an absence of programmatic research approaches addressing this important issue. Competitive interactions between hatchery and wild fish were observed to be complex, but studies researching approaches to reduce these interactions at all ecological scales during the entire salmon life history have been rare, and thus are not typically considered in hatchery management. Harvesting of salmon released from fishery enhancement hatcheries likely impacts vulnerable wild populations; managers have responded to this problem by mass marking hatchery fish, so that fishing effort can be directed towards hatchery populations. However, we noted that the effectiveness of this approach is dependant on accurate marking and production of hatchery fish with high survival rates, and it is not yet clear whether selective fishing will prevent overharvest of wild populations. Finally, research demonstrating disease transmission from hatchery fish to wild populations was observed to be equivocal; evidence in this area has been constrained by the lack of effective approaches to studying the fate of pathogens in the wild. We then reviewed several approaches to studying the economic consequences of hatchery activities intended to inform the social decisions surrounding programmes, but recognized that placing monetary value on conservation efforts or on hatcheries that mitigate cultural groups' loss of historical harvest opportunities may complicate these analyses. We noted that economic issues have rarely been included in decision making on hatchery programmes. We end by identifying existing major knowledge gaps, which, if filled, could contribute towards a fuller understanding of the role that hatchery programmes could play in meeting divergent goals. However, we also recognized that many management recommendations arising from such research may involve trade-offs between different risks, and that decisions about these trade-offs must occur within a social context. Hatcheries have played an important role in sustaining some highly endangered populations, and it is possible that reform of practices will lead to an increase in the number of successful programmes. However, a serious appraisal of the role of hatcheries in meeting broader needs is urgently warranted and should take place at the scientific, but more effectively, at the societal level.

1. INTRODUCTION

Enhancement is increasingly seen as an important fishery management tool (Leber *et al.*, 2005a), especially in light of the worldwide decline in wild fish populations. Broadly defined as the deliberate release of cultured organisms to increase population abundance for conservation or harvest objectives, enhancement of fish and invertebrate populations has been implemented extensively since the turn of the century. However, there has been considerable debate about the efficacy of releasing cultured organisms, the impact of these organisms on conspecific wild populations, and the relevance of this approach for meeting societal needs [reviewed in Taylor (1999a) and in Section 2]. Thus, enhancement has fallen out of favour as a management technique at various periods since it was first implemented. However, improvements in seed production, rearing technology, disease control, tagging and genetic and ecological approaches to management have invigorated renewed research in the field (Blaxter, 2000). These technological improvements have coincided with a changing philosophy; namely, that enhancement should be conducted in a scientifically based and sustainable manner (Leber *et al.*, 2005a), rather than providing a means of supplying unlimited fishery resources, or replacing extirpated natural populations without addressing the reasons for the decline.

Given this shift in philosophy and the renewed interest in the field, it is not surprising that several reviews and edited volumes on the topic have been published recently. In a comprehensive evaluation of marine fish enhancement, Blaxter (2000) has shown that success depends on the life history stage, the season at release, and the size of the enhanced region. However, doubt remains over whether enhancement can be used to recover declining fish populations occurring in the high seas (Blaxter, 2000). In their introduction to an edited symposium on the topic, Leber *et al.* (2005a) identified several key emerging issues associated with recent advances in the field, but pointed out that there are few examples of the successful implementation of these advances (Leber *et al.*, 2005b). This theme is echoed in a review of enhancement of marine invertebrates (Bell *et al.*, 2005); although programmes aim to either rebuild depleted populations or increase their productivity, objectives are infrequently identified and success is rarely measured, so any advances cannot be effectively evaluated.

A review of salmon enhancement activities adds an interesting dimension to discussions within the field. Salmon populations exhibit an extensive range of life history strategies (Allendorf and Waples, 1996; Quinn, 2005); they can be locally adapted to their rearing and spawning habitats (Taylor, 1991) and are genetically differentiated from each other on a fine scale (e.g., Waples *et al.*, 2001). Therefore, many enhancement efforts are aimed at discrete stocks or populations of salmon, and often take the form of hatchery programmes sited near spawning grounds. Additionally, programmes vary in their objectives and range from fishery enhancement to conservation hatcheries (Utter and Epifanio, 2002). There is considerable interest in the interactions between hatchery-produced fish and conspecific wild populations, many of which are endangered or declining (National Research Council, 1996; Parrish *et al.*, 1998). Above all, salmon are culturally and economically significant, and their management is usually driven by competing societal demands (Taylor, 1999a). Taken together, these issues provide a broad basis for evaluating a range of enhancement activities in a variety of species, each represented by a large number of independent stocks, and each aimed at fulfilling an assortment of societal needs.

Salmonid hatchery programmes have aroused considerable debate in the last few decades. Many critics have noted that hatcheries have failed to stem the decline of salmon stocks and, in some cases, have exacerbated this decline (Hilborn, 1992a; Larkin, 1974; Myers *et al.*, 2004; National Research Council, 1996). Biological problems that may arise following hatchery releases include changes in the genetic diversity of wild populations (Utter and Epifanio, 2002; Waples, 1991), risk of transmission of disease pathogens to wild stocks (Elliott *et al.*, 1997), exceeding the carrying capacity of streams and oceans (Beamish *et al.*, 1997; Levin *et al.*, 2001) and over-harvest of wild stocks due to mixed-stock fishing (Beamish *et al.*, 1997; Hilborn, 1985a; Unwin and Glova, 1997). On the other hand, a defence of hatchery programmes has been mounted on the basis that evidence of these problems is either lacking or the product of poor scientific rigour (Brannon *et al.*, 2004b; Heard, 2001), or that critics have specific social agendas (Brannon *et al.*, 2004b; Buchal, 1998; Robbins, 2004). The debate over hatchery programmes reached a peak in the mid-1990s, which led to advocates on both sides agreeing to rein in the rhetoric, if not substance, of their views (Hilborn, 1999; Schramm, 1996). However, in the United States, hatchery-related disputes moved to the courts after 2000, and legal challenges have included the interpretation of the language within the Endangered Species Act and a state's right to direct recovery efforts (*Alsea Valley Alliance*, 2001; *Maine v Norton*, 2003; *California State Grange*, 2005). Admittedly, these debates are rarely as polarized outside the United States, yet the character of these contests helps to illustrate the ecological and social implications of salmonid hatcheries, and how other societies fall along the spectrum of these views and responses.

The interaction between societal demands and science in the context of the hatchery debate is a complicated one. Social advocates on both sides often selectively employ scientific papers that further their view, while science is often confined to researching systems that have been established by public demand based on material needs (such as placing dams across rivers for hydroelectric power). In light of this complicated relationship, it is important to state from the outset that it is not our aim to enter the social debate on whether hatcheries should, or should not, exist. Many commentators have pointed out that hatcheries provide one of many tools that can be used in salmonid management (e.g., Mobrand *et al.*, 2005; Waples, 1999) and, in many cases, viable alternatives have rarely been offered. Thus, we acknowledge that enhancement activities are likely to persist in the foreseeable future, given their societal framework. Rather, we confine our review to the major social and scientific issues associated with the use of hatchery-raised salmon for conservation purposes and for fishery enhancement.

This chapter focuses largely on areas in which salmonid hatcheries could impact wild stocks. It should be pointed out that it is not the intent of this chapter to suggest that hatcheries should not have a role in salmonid enhancement activities, especially where their use represents an important means to recover critically endangered stocks. For example, it is likely that certain populations might well have gone extinct by this date without captive propagation programmes that have been largely successful (e.g., the Snake River sockeye salmon in the northeastern United States; Utter and Epifanio, 2002). We also attempt to identify major knowledge gaps associated with these issues. The topic is a large one, and cannot include all aspects of the debate, and thus we initiate our treatment by first describing the focus of this chapter.

1.1. Scope of the review

The term 'enhancement' takes in a wide variety of activities that humans have engaged in on behalf of salmon species and the fisheries that capture them. Thus, it is necessary to identify the kinds of activities that we will review, and those that we will not consider.

At one end of the continuum, there are 'habitat enhancement' projects that add woody debris to streams. These 'stream enhancement' efforts may or may not succeed in increasing fish densities, depending on whether the wood that was added remained in the channel, and whether it was needed in the first place (e.g., Cederholm *et al.*, 1997; Roni and Quinn, 2001). There have also been efforts at enhancing the productivity of rearing environments. Application of inorganic nutrients or the introduction of plant material- or marine-derived nutrients to freshwater may sometimes accelerate juvenile salmon growth (e.g., Hyatt and Stockner, 1985; Mason, 1976; Mundie *et al.*, 1983; Stockner and MacIsaac, 1996). Whether or not the fast growth in freshwater is translated into more adults (the real objective) is a more complex issue (Koenings *et al.*, 1993), but we will not review these studies.

In addition to activities directed at juvenile habitat or growth, there have been three main types of projects pertaining to the enhancement of reproduction: use of in-stream egg incubation boxes, spawning channels and hatcheries. The egg incubation box is used simply to protect developing embryos during their vulnerable stage by forcing the upwelling of water through gravel, where the eggs are placed. Spawning channels are artificial channels, supplied with water diverted from natural rivers or fed by groundwater and designed to optimize the conditions for spawning and incubation of embryos. In most wild populations, the survival from egg deposition to emergence is about 10–30%, depending on density and physical factors (Quinn, 2005), but survival rates in spawning channels can be about 50–80% (Essington *et al.*, 2000; Hilborn, 1992b). In species or populations where spawning habitat is the limiting factor rather than rearing space or food, the channels can be successful. Consequently, they are most widely used for pink, *Oncorhynchus gorbuscha*, and chum, *O. keta*, salmon (species that migrate to sea after emerging from the gravel) and sockeye salmon, *O. nerka* (that migrate to lakes) rather than for the species that rear in streams (e.g., coho, *O. kisutch*; and Chinook salmon, *O. tshawytscha*; steelhead trout, *O. mykiss* and Atlantic salmon, *Salmo salar*) because the production of these latter species is generally limited by rearing capacity rather than spawning capacity. We have elected to avoid reviewing the literature on spawning channels and outplanting of egg incubation boxes, and so will only consider enhancement projects that actually remove gametes from adult salmon for incubation (i.e., hatcheries). This is a very important distinction because some (though not all) of the issues related to hatcheries stem inexorably from the circumvention of natural processes of selection on the wild fishes such as spawn timing, nest site selection, preparation and defence by females and mate choice and competition by both males and females.

Our chapter does not include operations based on deliberately domesticated salmon that are maintained throughout their life cycle in aquaculture facilities for the purposes of food production. These types of operations have been the subject of a recent review (Naylor *et al.*, 2005). Although many of the issues associated with such activities are related to those examined here, fish from these facilities are not intended for deliberate release and it is the consequences of this management action that are the focus of this chapter.

Activities on anadromous salmonids in the genus *Salmo* (the Atlantic salmonids) and *Oncorhynchus* (the Pacific salmonids) will be examined, with a few examples from freshwater salmon within both genera and from *Salvelinus* (the charrs) (Table 2.1). However, this chapter places an emphasis on anadromous Pacific salmon for a number of reasons. First, the authors of this chapter are most familiar with this species. Many of the issues that will be addressed here are relevant to all species, and a comprehensive review of the issues in Pacific salmon, with supporting evidence from Atlantic salmon, is intended as illustrative. Second, Pacific salmon hatchery management has largely been under governmental control since the building of the first facility in California in 1871. Thus, the debate about enhancement has always been a very public one, and affected by legislation and court decisions. The use of Pacific salmon hatcheries involves public lands, and a large component of these operations is driven by the continued importance of commercial and recreational salmon fisheries. Third, most enhancement efforts in the eastern Atlantic are focused primarily on providing salmon for recreational fishing in the face of the decline of native populations and, to a

Table 2.1 Scientific names and common names of salmon species (family Salmonidae, subfamily Salmoninae) used frequently throughout this chapter

Genus	Common name (anadromous/ freshwater)	Scientific name
Salmo (the Atlantic salmonids)	Atlantic salmon	*S. salar*
	Sea trout/brown trout	*S. trutta*
Oncorhynchus (the Pacific salmonids)	Chinook salmon	*O. tshawytscha*
	Chum salmon	*O. keta*
	Coho salmon	*O. kisutch*
	Cutthroat trout (predominantly freshwater)	*O. clarki*
	Masou (cherry) salmon	*O. masou*
	Pink salmon	*O. gorbuscha*
	Sockeye salmon/kokanee	*O. nerka*
	Steelhead/rainbow trout	*O. mykiss*
Salvelinus (the charrs)	Arctic charr	*S. alpinus*

Infrequent examples are named in the text.

smaller extent, on harvest and conservation (Section 3). The more significant issues in Atlantic salmon are around the interactions between commercially farmed fish and wild stocks and, as we outlined above, outside the scope of our review.

Finally, we recognize that hatchery releases have substantial ecological impacts on the systems in which they operate, but do not review this aspect in detail. Instead, the chapter focuses primarily on the interactions between hatchery fish and their wild counterparts, since most hatchery operations are justified on the basis of supporting the very stocks with which they interact, either by directing harvest pressure away from wild stocks, or by supportive breeding for the recovery of weakened stocks. It is these justifications that will be largely examined here.

1.2. Motivations and objectives of hatcheries

The term 'hatchery' encompasses a broad spectrum of operations, each with different objectives and practises. Many critiques of hatchery practises fail to discriminate between these goals and hence the range of impacts that various activities will have on wild populations (Allendorf and Ryman, 1997). In order to provide a full evaluation of the state of knowledge of hatchery activities, it is therefore necessary to describe the different categories into which hatcheries fall. This attempt at definition should be qualified. It is recognized that hatcheries have rarely been categorized (Section 2) and many modern enhancement activities continue to lack clear defining objectives. Further, the purposes of hatcheries may change and yet may retain their founding broodstock. For example, a number of hatcheries in the northeast Pacific are defined as having conservation goals, but the majority of these were founded on the principle of providing opportunities for harvest. Thus, current hatchery practises are most likely to fall along a continuum of the definitions given here. Finally, many of the terms used below have been applied loosely. For example, 'supplementation' has been used to describe activities varying from conservation to fishery enhancement. 'Stocking' has been used in a generic sense to describe the release of cultured fish into the wild, but has also specific definitions in the context of enhancement, mitigation and conservation activities (Cowx, 1998). Here, we attempt to more clearly define many of these categories below.

Hatcheries are classified broadly by having either conservation or fishery objectives. The former are intended to restore extinct, endangered or threatened populations or to reduce the risk of extinction. The latter are used to increase population sizes for fishery opportunities. The aquaculture classification of Utter and Epifanio (2002) is largely followed here, with an emphasis on salmon hatcheries.

Captive broodstock hatcheries are conservation oriented, with the sole purpose of maintaining populations that cannot be supported in their wild habitat for even part of their life cycle (Utter and Epifanio, 2002). Typically, the broodstock is maintained in captivity until the population threats have been removed, at which point the captively reared fish will be restored. For example, populations of Atlantic salmon indigenous to the Iijoki and Oulujoki rivers in Finland have been maintained in captivity since dam construction removed suitable spawning habitat (Saisa *et al.*, 2003) and may be reintroduced as part of the International Baltic Sea Fishery Commission's 'Salmon Action Plan' to increase wild population returns. Sockeye salmon returning to Redfish Lake, part of the Columbia River drainage system on the west coast of North America, declined to very small numbers of returning adults from 1991 to 1996; all were taken into captivity, and a portion of the population has since been utilized in a continuing programme of reintroduction (Utter and Epifanio, 2002).

Supplementation hatcheries also share a conservation ethic. Waples *et al.* (2007) defined supplementation as 'the intentional demographic integration of hatchery and natural production, with the goal of improving the status of an existing natural population'. While the intention is to incorporate the broodstock into wild stocks, the degree of integration can vary, with different outcomes (Section 5.1). Supplementation activities have been implemented extensively on the west coast of North America in an attempt to mitigate losses due to anthropogenic activities such as dam construction, forestry, agriculture or urbanization (Section 3.1).

Production hatcheries, or *fishery enhancement hatcheries* (Utter and Epifanio, 2002), are hatcheries that seek to augment the abundance of salmon in order to increase fishing opportunities. 'Ocean ranching' has been defined as the release of 'juvenile specimens of species of fishery importance raised or reared in hatcheries and nurseries into the sea for subsequent harvest at the adult stage or manipulating fishery habitat to improve growth of the wild stocks' (Mustafa, 2003), which can often include domesticated stocks, and thus falls under this category. One potential outcome of such activities is that the resulting demographic increases may redirect harvest pressures away from natural production. In many cases, the wild populations are viable. Production hatcheries are used extensively throughout the world. For example, many European countries release anadromous Atlantic salmon and brown trout (*S. trutta*) populations; many hatchery strains are derived from exogenous stocks. The pink salmon fishing industry in Alaska is supported by releases from production hatcheries in Prince William Sound (PWS; Section 4).

Mitigation hatcheries are production hatcheries that have typically been founded to compensate for lost harvest opportunities following substantial reduction or extirpation of an indigenous stock due to losses of habitat or other anthropogenic activities (Utter and Epifanio, 2002). Such hatcheries have been established with the understanding that the habitat that is essential for part of the salmon life cycle will not be replaced within the predictable future, and thus continuation of the population is dependant on artificial propagation. The most extensive programme in this category is the chum salmon programme operated in Japan (Section 4). In many cases, mitigation hatcheries are maintained in order to meet a mandate imposed by prior rights of a group to the fishery. For example, access to the Chinook salmon fishery was lost by the native peoples of the Columbia River Basin following the construction of the Grand Coulee Dam, and mitigation hatcheries were constructed in response to tribal treaties (Utter and Epifanio, 2002). Given increasing concern that endangered or threatened stocks may be caught in mixed-stock fisheries (Section 5.4), the release of hatchery fish at a remote acclimation site has been explored. In the Columbia River, for example, an ongoing programme has placed hatchery juveniles into a net pen at a location that has not been frequented by migrating endangered salmon stocks (ISRP/IEAB, 2005). The project's intent is that the fish acclimate and return to the remote site where they can be harvested, thus reducing risk to the endangered wild stocks.

Hatcheries providing fishing opportunities for non-indigenous fisheries (*Introduced fish*) are production hatcheries (including 'put and take' aquaculture) operated to provide harvest or recreational fishing opportunities on species that are exotic to the region in which they are released (Utter and Epifanio, 2002). For example, rainbow trout has been extensively introduced to countries in the Southern Hemisphere, and Chinook salmon has been introduced to the North American Great Lakes and New Zealand. Many of these operations involve a single introduction, while others are maintained by hatchery programmes (e.g., Chinook salmon in the Great Lakes) with the notion that the introduced species may go extinct once such activities cease.

1.3. Content overview

In the following sections, we provide a social context for an evaluation of hatchery operations through an overview of the history of hatchery activities and the political dynamics associated with hatchery programmes. We then provide a survey of the geographical extent of anadromous and freshwater hatchery programmes throughout the world. In an attempt to understand the impacts of such programmes, we evaluate in detail the types of biological risks that hatchery programmes may pose to wild stocks of salmon species and return to the social aspect of such programmes by examining the economic issues associated with hatchery programmes. The chapter ends with a discussion on the risks associated with conservation and fishery enhancement hatcheries, and on the social drivers and costs of hatchery activities.

2. HISTORICAL OVERVIEW OF HATCHERY ACTIVITIES

Western salmonid fish culture dates to eighteenth-century Westphalia. In 1747, army officer and naturalist Ludwig Jacobi used ancient Asian techniques to fertilize and rear trout in an artificial environment, but not until he published his memoirs in 1770 did his achievements gain notice. In the next century, a number of Europeans emulated his efforts, including Karl Lund, Karl Vogt, John Shaw, Joseph Rémy and Antoine Géhin. Each refined and expanded upon Jacobi's work by innovating new methods for raising an array of freshwater and anadromous species. These were limited efforts by individual enthusiasts and scientists, people primarily interested in studying and reproducing small stocks of fish for fulfilment or profit rather than for professional or industrial interests (Marsh, 1857; Prince, 1900).

The development of a hatchery programme, in the modern sense of the systematic management of fish and fisheries, required a more institutionalized approach. France was the first to adopt this tack. In 1850, inspired by the work of Rémy and Géhin at Bresse and the writings of naturalist Armand de Quatrefages, the French Minister of Agriculture built a fish-breeding station at Huningen to repopulate the Rhine and Rhône rivers. Soon Switzerland, Germany, England and Scotland had established similar efforts to restore their fisheries. In most cases, these hatcheries were designed to serve both angling and commercial interests, and while none produced immediate, demonstrable successes in rebuilding stocks, they represented a new movement in fisheries policy that drew the attention of North Americans. Interest in fish culture began relatively late in Canada and the United States. The first documented case of reproducing trout was by Ohioan Theodatus Garlick in 1853. This work quickly gained notice. Fishmongers and anglers saw a hope for reversing decades of decline in the fisheries. As a result, they lobbied legislators throughout the eastern states to establish fish hatcheries, and from 1855 to 1857, Massachusetts, Connecticut and Vermont commissioned studies on approaches to restore local fisheries. Each report became a treatise on the technical and socio-political implications of breeding fish, and each concluded that while fish culture had not yet restored a troubled fishery, the technology held tremendous promise for ameliorating the material consequences of progress.

Government support for hatchery programmes did not begin in the United States until the end of the Civil War. In 1865, New Hampshire built the first state-run hatchery, and California, Connecticut, Maine, New Jersey, New York, Pennsylvania and Rhode Island followed by 1870 (Bowen, 1970). These operations were primarily dedicated to game fisheries. The major expansion of fish culture in the next decade was more tied to commercial interests however. In 1867, at the request of several New England fish commissions, a for-profit fish culturist named Seth Green bred shad eggs on the Connecticut River; the next year he extended this work to the Hudson, Potomac and Susquehanna rivers (Goode, 1881; Norris, 1868). In 1871, Charles Atkins and Livingston Stone persuaded the state of Maine to build a hatchery at Bucksport specifically for hatching Atlantic salmon, and Frank Clark hatched whitefish on the Great Lakes in 1872 (Milner, 1874; Stone, 1897).

Canadian fish culture loosely paralleled American activities. In the late 1850s, Richard Nettle first hatched brook trout and Atlantic salmon in Quebec city. By the mid-1860s, enthusiasts were hatching these species and lake herring on the St. Lawrence and Great Lakes. The most prominent culturist was Samuel Wilmot, a zealous self-promoter who billed himself as the leading fish culturist in North America. In 1866, he persuaded the province of Ontario to hire him as a fishery officer and fund his hatchery at Newcastle on Lake Ontario. Two years later, the Dominion of Canada took over the hatchery and made Wilmot an officer of the Department of Marine and Fisheries. In the early 1870s, he built additional salmon hatcheries on the Restigouche (1872), Miramichi (1873), Gaspe (1874) and Tadoussac (1875) rivers, and in 1876 he was promoted to Superintendent of Fish Breeding for Canada. The Dominion built its first hatchery for Pacific salmon on the Fraser River in 1884. Wilmot overstated his achievements on occasions—he had not been the first to hatch salmon or whitefish—but he was, without doubt, the driving force behind federalization of artificial propagation in North America (Prince, 1900; Lasenby *et al.*, 2001).

Influenced by Canada's hatchery programme, the US Congress soon followed suit. It created the US Fish Commission (USFC) in 1871, and the following year the first commissioner, Spencer Fullerton Baird, assigned Livingston Stone to transplant salmon eggs from the Sacramento River to eastern streams. In 1873, Baird hired Seth Green to plant shad in Midwestern streams and the Sacramento River. Other American fish culturists refined methods for inseminating and incubating eggs, and Baird turned his USFC employees into an army of researchers, surveying habitat and species abundance, investigating egg development and experimenting with fish feeds. As in Canada, federal support for fish culture grew. By the 1880s, Congress was funding hatcheries from the Bay of Fundy to San Francisco Bay, from the Columbia River to the Savannah River and from the Gulf of Mexico to the Great Lakes. By the end of the century, Canada and the United States had built extensive hatchery programmes. Almost every major fishing stream was affected by at least one federal, state, provincial or private hatchery, and fish culture had become an intrinsic tool of managing game and commercial fisheries across North America (Allard, 1978).

Both countries also conducted extensive fish transportation programmes. The motivations for transplant programmes were complex. Some of it was driven by emigrants' desires to recreate the ecologies of home or, as Wisconsin's Commissioners of Fisheries boasted in 1888, in hopes of creating one vast 'Summer Paradise' (quoted in Bougue, 2000; see also Lampman, 1946). Economic opportunity was another major influence in shipping salmon around the world (Taylor, 1999a), and, as Spencer Fullerton Baird himself admitted in 1877, political considerations also drove transplant projects: 'The object is to introduce [fish eggs] into as many states as possible and have credit with Congress accordingly. If they are there, they are there, and we can so swear, and that is the end of it' (quoted in Allard, 1978). Using railways and steamships, hatchery programmes sent species to every corner of the continent and beyond. In the last quarter of the nineteenth century, the USFC and Canada Department of Marine and Fisheries transplanted a menagerie of species. Pacific salmon were transplanted to the Great Lakes, South Dakota's Belle Fourche River, and the Great Salt Lake, not to mention Europe, Asia, South America and Australasia (Colpitts, 2002). By 1900, global hatchery ecology was emerging in which salmonids played a key, but hardly singular, role. Brown trout were shipped from England to California, California Chinook salmon were sent to New Zealand, Japanese koi (*Cyprinus carpio carpio*) were cultivated in Massachusetts, Rhode Island shad were released in Oregon streams, Oregon steelhead were exchanged with Germany, German carp (*C. carpio carpio*) were placed in the Great Basin and black bass were released just about everywhere (Allard, 1978; Bogue, 2000; Bowen, 1970). Salmonids were far from the only species introduced to new environments.

The paradox of most hatchery programmes was that institutional successes went hand-in-hand with ecological disaster. Despite growing fiscal support—Congress increased the Division of Fish Culture's budget from $25,000 in 1873 to $331,000 by 1900—optimism was deserting fish culturists (Cart, 1968). North American and European salmon runs had been declining for centuries (Netboy, 1980). Whitefish populations in the Great Lakes had collapsed in recent decades, as had shad and alewife stocks along the Atlantic (Bogue, 2000; McPhee, 2002; Steinberg, 1991). Shad (*Alosa sapidissima*) and striped bass (*Morone saxatilis*) were colonizing west coast streams, but few markets existed for these species and some observers worried that exotics would disrupt native species. German carp were denuding rearing habitat for western North American trout (Langston, 2003), and brown trout and rainbow trout were displacing indigenous species in Australia and New Zealand (Crowl *et al.*, 1992). The more things fell apart, the more politically potent hatchery programmes seemed. By the early twentieth century crises had become fish culture's *raison d'etre*. Declining stocks and degraded habitat made artificial propagation the default solution for many governments. And if the results often fell short, the achievements of these programmes were no less significant. North American fishery agencies had become the gold standard for fishery management. The USFC had developed into a model agency for supporting fisheries through economic surveying, scientific research and artificial propagation, and professional scientists were turning the American Fisheries Society and, after 1912, the Biological Board of Canada, into premier organizations for fisheries science (Johnstone, 1977; Smith, 1994).

The principal exceptions to the mounting problems of hatchery work were a select few game fish species. Brown trout (*S. trutta*), rainbow trout (*O. mykiss*), bass (*Micropterus dolomieu* and *M. salmoides*), catfish (*Ictalurus furcatus, I. punctatus, Ameiurus catus*), crappie (*Pomoxis nigromaculatus*), perch (*Perca flavescens, Morone americana*) and pike (*Esox lucius*) adapted well to pond culture, but, equally important, each also had enthusiastic angling constituencies. In Europe, angling had been a primary motive for planting brown trout and Atlantic salmon since the 1700s. Since the majority of streams were privately owned, most releases were performed by individuals and fishing associations. Conditions in Japan and North America were different. Most waters were publicly owned, so both individuals and the state released fish into the waterways. In Japan, for example, the Agricultural Bureau initiated hatchery work in 1878 on streams in Niigata-ken, Nagano-ken, Ibaraki-ken and Hokkaido. Budgets and plantings grew significantly by 1900 (Imperial Fisheries Bureau, 1904). Canada followed a slightly different path. At first small, privately run hatcheries operated in the Maritimes, Quebec and Ontario, and a few provinces gained some authority over fisheries by 1900. The federal government retained primary authority for oceans and ultimate authority for all other fisheries, however (Thompson, 1975). Thus, similar to Japan, the Dominion of Canada operated in support of both angling and commercial interests well into the twentieth century.

Hatchery development in the United States was more complicated due to a constitutional division of authority. The federal government held jurisdiction of seas, navigable rivers, and territories, but states ruled all other waters including the oceans within three miles of the coast. In practise, this meant that the USFC and US Bureau of Fisheries (USBF) propagated commercial species that frequented the seas or interstate waters such as the Great Lakes and Columbia River (Allard, 1978; Taylor, 1999a). Federal hatcheries planted game fish in national parks and federal forests, as well as across Alaska, but by 1900 states were taking over the primary responsibility for much of the hatchery work (Pritchard, 1999). Fishery agencies were evolving into a huge apparatus for breeding and distributing fish. Large and growing bureaucracies existed in nearly every state, and an immense amount of fish were bred and planted each year by fish culturists (Lampman, 1946; Reiger, 2001; Taylor, 1999a).

The next half-century was a period of elaboration rather than change. The size and scope of fishery agencies continued to grow as stock depletion and habit decline accelerated after 1900. The policy of compensating for problems with fish culture, begun in New England in the 1860s, extended to the Pacific Northwest in the 1910s when Washington State adopted an 'in lieu' policy that would eschew fish-ways if the dam owner funded a hatchery (Steinberg, 1991; Taylor, 1999a). Although few governments made this formal policy, all were increasingly inclined to mitigate losses rather than restrain development. When alewife (*A. pseudoharengus*), eel (*Anguilla rostrata*), salmon, shad and sturgeon (*Acipenser transmontanus*) populations dropped because of habitat loss, agencies in Canada, France, Great Britain, Ireland, Japan, Russia and the United States responded by advocating fish-ways and hatcheries. Few wild fish populations recovered, but the bureaucracies overseeing them thrived (Netboy, 1980; Pritchard, 2001; Taylor, 1999a).

Hatchery programmes also experienced an institutional mitosis. The fisheries had been torn by rivalries for centuries. Towards the end of the nineteenth century, state legislatures in the United States began to formalize the divisions between sport and commercial interests in separate fish and game departments. Fish culture was influenced by these events as it was embedded in such agencies. Individual hatcheries began to specialize, serving the desires of constituencies interested only in market or game fish, or specifically in one species. In the Pacific Northwest, for example, Oregon's Fish Commission began to favour Chinook salmon in coastal streams where coho had been the dominant native fish, while the Game Commission planted bass and walleye (*Sander vitreus*) in inland streams where salmon and trout had predominated (Taylor, 1999a). Transplanting coho to Lake Michigan in the 1960s precipitated similar upheavals in the Great Lakes (Chiarappa and Szylvian, 2003). Institutional specialization and ecological reorganization occurred across many Northern Hemispheric fisheries during this period, including Hokkaido Island, Vancouver Island, Yellowstone National Park and the Barents Sea and White Sea (Harris, 2001; Imperial Fisheries Bureau, 1904; Pritchard, 2001).

Scientific research also became an increasingly important institutional activity. The USFC had been created as a research agency in 1871, and Commissioner Baird insisted that research remain a high priority even as fish culture dominated budgets (Allard, 1978). Annual reports included essays by top scientists, and the *Bulletin of the Bureau of Fisheries* was a science publication from its inception in 1881. The other major research publication in the United States was, of course, the *Proceedings of the American Fish-Cultural Association* and its successor, the *Transactions of the American Fisheries Society* (Smith, 1994). The Biological Board (later the Fisheries Research Board) of Canada began its own research programme in 1912 (Johnstone, 1977), and Europeans had developed a tradition of scientific cooperation long before the International Committee on the Exploration of the Seas (ICES) formed in 1902 (Rozwadowski, 2002). In addition, various state and provincial fishery agencies in the United States and Canada began their own research programmes (Taylor, 1999a).

The impact of this science on hatchery operations was uneven. Some research proved functional, such as designing efficient fish-ways and fish screens, understanding predators and parasites and refining effective and economical feeds (Bowen, 1970; Eicher, 1970; McHugh, 1970). Fish tagging studies confirmed the home-stream theory for salmon and influenced fishing treaties (Taylor, 1999a). Administrators of hatchery programmes in Canada and the United States embraced this work enthusiastically, but they rejected critical research. Harley White's study of Prince Edward Island trout (White, 1924), Willis Rich's statistical analysis of Columbia River hatcheries (Rich, 1922) and Russell Foerster's work of Cultus Lake sockeye (Foerster, 1936) all cast doubts on claims that fish culture had made significant differences in the size of salmonid populations. Although economic considerations were also important, this research did influence decisions to halt hatchery work in British Columbia and Alaska during the 1930s. Fish culturists responded by attacking White and ignoring the broader implications of his research (Johnstone, 1977; Taylor, 1998b). By 1950, salmonid hatchery programmes in North America were on a path best described as scientific yet without scrutiny (Hilborn and Winton, 1993; Lichatowich, 1999; Taylor, 1999a). Similarly aggressive hatchery programmes have been initiated around the Baltic Sea in recent decades, but here, too, familiar problems with disease, interbreeding, mixed-stock fisheries and declining wild populations have emerged (Khristoforov and Murza, 2003; Paaver *et al.*, 2003).

Research during the 1940s and 1950s created the technical and intellectual foundation of the last half-century. Studies of parasites and diseases, and advances in medical and food science led to new prophylactic treatments. Fish culturists devised ways to address epizootics, and extruding machines produced pelleted feeds that avoided age-old problems with nutritional deficiencies and contamination (Stickney, 1996). These innovations allowed fish culturists to raise more fish, more economically for far longer. As hatcheries began to raise greater numbers of much larger fish, fishery bureaucracies expanded again. Great Lakes managers started replacing failing whitefish stocks with trout, and west coast hatchery workers used new feeds to retain Pacific salmon to smoltification (Chiarappa and Szylvian, 2003; Taylor, 1999a). Meanwhile, the Scandinavians succeeded in raising rainbow trout and then Atlantic salmon from eggs to harvest. By 1960, a far more technically based era of salmonid culture had emerged (Sedgwick, 1982).

Developments in North America since 1960 have exposed lingering problems with hatchery programmes. Practises learned from the commercial farming of Atlantic salmon, rainbow trout and several Pacific salmons, and the transporting of juvenile Pacific salmon around dams with trucks and barges were regarded as significant advances in the 1960s and early 1970s. The salmon hatchery programme was even revived in British Columbia, where Canada's Department of Fisheries and Oceans (DFO) constructed a number of production hatcheries, and the International Pacific Salmon Fisheries Commission (IPSFC) began to experiment with artificial spawning channels (Mead and Woodall, 1968; Roos, 1991). The appearance of success faded in the 1970s as worries surfaced about the deleterious effects of mixed-stock fisheries, genetic interactions with wild stocks, threats of disease transmission, mass hatchery releases out-competing wild stocks and continuing declines in many fisheries (Lichatowich, 1999; Orr *et al.*, 2002; Taylor, 1999a). Many western inland trout and Pacific salmon stocks have declined due to habitat loss, competition from and hybridization with exotic species (Cone and Ridlington, 1996; Leary *et al.*, 1995). Hatcheries on the Great Lakes produced so many lake trout and Pacific salmon that they annihilated the last significant whitefish stocks (Chiarappa and Szylvian, 2003). In addition, the collapse of Labrador's Atlantic salmon fishery in the 1970s revealed the inability of hatcheries in the eastern United States and the Maritime Provinces to compensate fully for the effects of intense harvests and declining habitat (Netboy, 1980).

During this period, hatchery programmes in Europe and Scandinavia showed mixed results. In the 1970s and 1980s commercial salmon farms in Norway, Scotland and Ireland gained a foothold in the marketplace due to declining salmon fisheries in the western Atlantic and northeastern Pacific. The Norwegian salmon farming programme at the time also aided small, outlying communities; however, a market collapse in the 1990s, caused in part by competition from a rapidly expanding Chilean salmon aquaculture industry, led to industry consolidation by a few corporations and growing concerns about the ecological impacts of industry practises (Milstein, 2003). More recently, efforts to rebuild extinct runs in Belgium's Meuse River basin revealed, once again, that the success of artificial propagation depends on healthy habitat and competent fish passage technologies (Prignon *et al.*, 1999), while work on the Asón and Nansa rivers in Spain demonstrated that transplanted salmon stocks fare more poorly than native wild stocks (Verspoor and de Leaniz, 1997). Species hybridization between Atlantic salmon and trout populations in Sweden has been attributed to the release of too many fish by hatcheries (Jansson and Oest, 1997), and hatcheries throughout the Gulf of Bothnia have contributed to genetic homogenization in wild Atlantic salmon populations (Khristoforov and Murza, 2003; Paaver *et al.*, 2003; Vasemägi *et al.*, 2005).

The persistence of these problems, most of which have plagued salmonid hatcheries for a century or more, has inspired ever more urgent calls for reform and even termination. Critics have demanded that salmonid hatcheries be independently evaluated, that hatchery managers define goals which are rigorous and testable and that administrators develop policies based on the best available science (Brown, 1982; Lichatowich, 1999; Mobrand *et al.*, 2005; National Research Council, 1996; Taylor, 1999a). At the same time, however, it is clear that some wild salmonid stocks are in such great peril that the only hope for recovery seems to be the sort of intensive hatchery programmes that exacerbate problems within the region (Schiewe *et al.*, 1997). Thus, the last 15 years has been a period of reassessment. History casts a troubling light on the practises and goals of many salmonid hatchery programmes, but no consensus has emerged yet about the future of these programmes.

3. POLITICAL DYNAMICS OF HATCHERY PROGRAMMES

Although usually considered a scientifically based activity, salmonid hatcheries must also be understood as political technologies fundamentally shaped by economic and cultural concerns. Scientists have been key players in creating and shaping hatchery programmes, and fish culturists have conducted important research, yet the history of these programmes reveals that science has often played only a secondary, legitimizing role in policy-making, or has been implemented to maintain the *status quo*. Social and economic politics has been the primary influence on government-sponsored hatchery programmes in the last two centuries. Thus, examining the historical context of the political aspects of fish culture is essential for understanding the development and consequences of salmonid hatcheries during this period.

This historical perspective is particularly crucial in the current, highly politicized climate that surrounds salmonid hatcheries. In recent years some programmes have earned withering criticism. Scholars have cited a number of problems, including insufficient scientific rigour, economic worth and ecological viability in many enhancement programmes (Anonymous, 2004; Hilborn and Eggers, 2000; Myers *et al.*, 2004; National Research Council, 1996). With less care, critics have also tried to explain the technology's origins by variously blaming zealous founders, short-term thinking and even Francis Bacon for replacing a holistic appreciation of nature with instrumentalist thinking (Cone and Ridlington, 1996). The disparity between careful studies of technical issues and vague assertions about historical roots has hindered our understanding of why science has not been a stronger guide in hatchery policies (McEvoy, 1986).

Closer attention to the past illustrates how thoroughly blurred politics and science were in early hatchery programmes. From the beginning, proponents of hatcheries noted that manual fertilization of fish eggs produced far greater hatch rates than natural reproduction. Many were led by an arithmetical logic to predict astonishing increases in fish populations by even meagre efforts. According to US Fish Commissioner Spencer Fullerton Baird, fish culture would allow the government 'not only to maintain the present supply of fish, but to increase it if desirable' (Baird, 1874). Framing these insights in agrarian terms, proponents argued that an acre of water was more productive than one, five, or ten acres of land. One even insisted that 'one acre of the waters of any salmon stream in Oregon . . . is worth more as a medium for the product of a food supply than forty acres of the best land in the State' (Hume, 1893). Such boasts drew notice in many countries, but what made fish culture most appealing for government officials were its political implications. Few could resist a technology that French scientist Jules Haime claimed (Marsh, 1857) was 'destined to solve one of the important terms of the great problem of cheap living' (McPhee, 2002).

The cultural context in which fish culture emerged was another factor in its popularity. Although the rhetoric surrounding fish breeding emphasized bountiful harvests, contemporary politicians were less motivated by Malthusian fears of hunger than by the growing conflicts between aquatic and terrestrial interests. George Perkins Marsh, who was squarely on one side of this contest, explained to Vermont's legislature in 1857 that 'We cannot destroy our dams, or provide artificial water-ways for the migration of fish. . .; we cannot wholly prevent the discharge of deleterious substances from our industrial establishments', nor was it probable 'that any mere protective legislation, however faithfully obeyed, would restore the ancient abundance of our public fisheries'. For Marsh and others the 'final extinction of the larger wild quadrupeds and birds, as well as the diminution of fish, and other aquatic animals, is everywhere a condition of advanced civilization and the increase and spread of a rural and industrial population' (Marsh, 1857). Destruction was thus the sad but inevitable cost of progress.

Most people exploring the feasibility of fish culture programmes were not worried about an imminent implosion of food sources. Rather, it was growing contests over dwindling fish stocks that forced politicians in many countries to address the issue. In other words, it was the *political* implications of finite resources, not hunger, which first inspired modern hatchery programmes. Conflicts among fishers led France to build a government hatchery at Huningen in 1850 to repopulate the Rhine and Rhône rivers. Lobbying by sport and commercial interests led New England states and Canada to fund trout, shad and salmon work during the 1860s (Prince, 1900; Reiger, 2001), and tourism agendas influenced Japan to build a hatchery on Lake Chuzenji in the 1890s (Imperial Fisheries Bureau, 1904).

Economic possibilities helped leverage funding, but as Spencer Baird noted in an 1875 letter to the US Senate, the tangled problems of regulation were also salient. 'In the United States', he observed, 'it has always been found very difficult to enforce laws in regard to the fisheries. When passed by the States they involve an extensive police for their execution', and, crucially, no state had built such a force. Thus he 'unhesitatingly' recommended that instead of the passage of protective laws which cannot be enforced except at very great expense and with much ill feeling, 'measures be taken . . . for the immediate erection of a hatching establishment on the Columbia river, and the initiation during the present year [1875] of the method of artificial hatching of these fish' (Baird, 1875).

Here were the political underpinnings of the modern hatchery. Government officials in many countries, most of whom knew or cared little about fish or about fish culture, nevertheless supported large government budgets for these programmes not simply because the technology promised to sustain fisheries but because Haime and Armand de Quatrefages in France, Frank Buckland in Britain, Samuel Wilmot in Canada and Marsh and Baird in the United States assured officials that hatcheries would avert the social conflicts between declining fish stocks and modern development (Bogue, 2000; Gardner-Thorpe, 2001; MacCrimmon, 1965; Prince, 1900; Taylor, 1999a). For governments and the public alike, much of fish culture's appeal emanated from its panacean qualities (Taylor, 1999a). Hatcheries seemed to alleviate the need to make hard choices about limiting access to fish or habitat.

Yet governments did make choices and did intervene, and one of fish culture's first impacts was on property rights. By 1850 many state legislatures in the United States had already forced dam owners to maintain fish-ways to protect migrating species (Steinberg, 1991). Such limitations became precedents for further restrictions to facilitate artificial propagation. Between 1861 and 1865 the British Parliament passed acts for England, Ireland, Scotland and Wales that exempted fish culturists from regulations and limited private claims on some Scottish and Irish streams (Great Britain, 1861, 1862, 1863, 1865). Americans were more hesitant. Marsh advised Vermont legislators to rely 'upon the enterprise and ingenuity of private citizens' and to create economic incentives by according property rights to fish produced by entrepreneurial hatcheries (Marsh, 1857). Vermonters did not agree, believing that fish and game should remain free until capture (McEvoy, 1986). The same held true across the United States, Canada and Japan, but experiences varied in European nations. In countries with customs of privatized fish and game, parliaments had to finely tune rules to specific bodies of water before initiating public or private hatcheries during the last two centuries (Prat, 1998).

Even then, however, fish culture did not prevent further restraints on people's interests in fish, water and land. One unavoidable conflict created by hatcheries was the need to harvest fish. The very effort to enhance fish stocks put fish culturists in conflict with other resource users. One hatchery on Oregon's Clackamas River inspired repeated conflicts because the hatchery weir blocked both migrating salmon from upstream settlers and logs floating to downstream lumber mills (Taylor, 1999a). Far more common were the ways hatcheries abetted the dispossession of resources. In Canada (the Maritimes, St. Lawrence and British Columbia), in the United

States (New England, the Great Lakes and Pacific Northwest) and in Japan (Hokkaido Island), hatcheries divided indigenous peoples from their salmon, trout and whitefish fisheries (Harris, 2001; Newell, 1993; Parenteau, 1998; Taylor, 1999a; Walker, 2001). In 1877, for example, Livingston Stone evicted Clackamas Indians from their fishery to prevent competition with his hatchery (Taylor, 1999a). Over time, hatcheries built to mitigate dams also reorganized the spaces of reproduction in ways that deprived Native peoples of their historic fisheries (Allen, 2003; Evenden, 2004; Taylor, 1999a). In a few instances, such as the introduction of Pacific salmon to the Great Lakes, exotic transplants for the benefit of recreational anglers also undermined commercial and aboriginal fisheries (Chiarappa and Szylvian, 2003). In recent years, however, the lines of these conflicts have shifted. In Europe, notably in Britain, and in North America, growing concerns about the genetic implications of declining stocks of wild salmonids have increasingly pitted conservation groups against the only remaining significant group of harvesters: anglers.

Another consequence was that salmonid hatcheries became contested prizes. Relentlessly shrinking fish stocks exacerbated existing tensions among fishers, and the rarer a population or species became, the more hatcheries became an explicit prize in political battles. In Canada and the United States, commercial and sport fishers engaged in what was essentially an ecological tug of war, battling over the control of hatcheries and the release of game and commercial species. In Oregon and Washington, industrial fishers also fought over which hatcheries and rivers would receive financial support (Parenteau, 1998; Taylor, 1999b). In the Great Lakes, Pacific Northwest and Japan, commercial and sport fishers also tried to deny aboriginal fishers access to hatchery fish (Blumm, 2002; Chiarappa and Szylvian, 2003; Shigeru, 1994). The advent of salmon aquaculture has had similar implications in Norway, where commercial fishers were excluded from harvesting Atlantic salmon to protect sport and farming interests (Otterstad, 1998). On the other hand, Alaskans chose to bar Atlantic salmon aquaculture from their state and restrict activities to 'private, non-profit' (PNP) hatcheries, fearing that the ecological and economic destabilizations that have accompanied farming operations elsewhere would negatively affect their Pacific salmon fisheries (Herbst, 2003).

Such consequences illustrate why technology must be understood within its historical context. Fish culture was not inherently racist or classist, even if some fish culturists were bigots (Chiarappa and Szylvian, 2003), but when hatcheries were used to serve the interests of some at the expense of others, then technology was politicized. This held true not only in those internecine battles that plagued sport and industrial fisheries during the last two centuries (Jacoby, 2001; Thompson, 1975), but, more insidiously, it also applied to industrialization. Fish hatcheries meshed seamlessly with an ideology of production that defined value narrowly in terms of economic wealth and regarded development as a natural good. Once industrial growth emerged as the ultimate goal, fish culture thrived politically because it promised to enable such an agenda. This partnership between fish culture and development began very early. The first hatcheries were built in Europe and eastern North America in the 1850s and 1860s to stem declining fish stocks due to habitat loss and industrialization (Kinsey 2006; Netboy, 1968; Pisani, 1984; Smith, 1994). In western North America, fears of overfishing were the fulcrum for establishing hatchery programmes (Harris, 2001; Taylor, 1998b). In all cases, fish culture was popular because neither the public nor legislators wanted to regulate economic activity. This pattern of relying on technological solutions was a deliberate, politically influenced choice that continued throughout the twentieth century (Meffe, 1992). After 1910, state, provincial and federal governments allowed entrepreneurs to mitigate damaging activities by funding state-run fish hatcheries (Blumm, 2002; Evenden, 2004; Harris, 2001).

This 'in-lieu' policy saw its most aggressive application with dam-building programmes in Washington State on the Cowlitz, Lewis, White Salmon and Columbia rivers, but it was a popular solution from Japan to Western Europe. In 1923, Herbert Hoover declared 'We have only to preserve and increase the supplies of our fish by moderate restraint and scientific propagation' (Taylor, 2004). In the 1950s, France dammed the Rhône for navigation and hydroelectricity and hoped hatcheries would mitigate fisheries losses (Pritchard, 2001). In the 1960s, the Hokkaido Development Agency confiscated Ainu lands to build the Nibutani Dam for the sake of national progress (Sonohara, 1997). The culture that inspired each event has not changed in many cases. In 2003, the US President George W. Bush insisted that dams posed no problems for salmon runs (Reichmann, 2003). In all cases governments essentially institutionalized George Perkins Marsh's assumption that damage to wild stocks was an unavoidable consequence of progress. In a few places such as the United Kingdom, fishery institutions have begun to embrace a more risk-adverse approach to managing fragile stocks of salmonids, but in these cases the role and operation of hatcheries has also undergone significant change. Hatchery programmes have continued to thrive because they remain the most politically appealing, least controversial way to address the material consequences of development.

The political appeal of fish hatcheries was underscored by the technology's resistance to scientific criticism. Researchers have noted many basic flaws with fish culture. In the 1890s Knut Dahl, Johan Hjort, Ernest Holt and John Moore cast doubt on the efficacy of fish culture by citing poor statistics, insufficient controls and inconsistent results. These were leading European scientists, yet government officials ignored them in favour of voices that said what politicians wanted to hear (Smith, 1994). Criticism nevertheless increased with time. In the 1910s Americans Barton Warren Evermann and Willis Rich lodged similar complaints, as did Canadians

Russell Foerster, William Ricker and Harley White in the 1920s and 1930s (Taylor, 1998a, 1999a). After World War II, scientists expanded the litany of criticisms to include problems related to genetics, mixed-stock fisheries and habitat loss. Peter Larkin and James Lichatowich have been only two of many scientists who continued to point out the fundamental problems with salmonid enhancement in recent decades (Larkin, 1974; Lichatowich, 1999).

More than any other aspect of fish culture, it has been the selective acceptance of this criticism that underscores the importance of a broad historical perspective. Calls for 'better science' to guide hatchery programmes sound sensible (Koenings, 2000; Parent, 2003), yet the more we consider the tangled history of science and politics, the less science seems able to resolve basic problems with these programmes. Calls for adaptive management—for framing policies around assumptions of a complex and unpredictable nature informed by incomplete and evolving knowledge—suggest growing acceptance of this messy state of affairs. Yet even this approach leaves many issues unresolved (Lackey *et al.*, 2006; Langston, 2003). An underlying assumption of adaptive management has been that, if not now then eventually, science *will* lead (Lee, 1993). The problem is not simply that science has never been a primary guide, but that our yearning for objectivity ignores the import of history. Not only has politics intrinsically shaped the agendas and practises of modern salmonid hatcheries, but the consequences of these actions have also narrowed managers' options. For example, the use of spawning channels and acclimation ponds were not simply new scientifically based technological approaches to hatchery problems but also politically based decisions to rely on environments that mimic natural conditions rather than on wild environments themselves. Longing for objective science obscures the historically produced circumstances that continue to constrain both our policy options and the ecological and social consequences of our choices.

This is not a call to abandon dispassionate science for subjective politics, but a request that readers learn to recognize the intrinsic social and ecological implications of salmonid hatcheries. Science is a necessary tool for developing effective practises, but it cannot resolve the social politics that have framed the structure and intent of fish culture policies since the mid-nineteenth century. Thus, expectations that more science will necessarily lead to better policies tends only to mask the social implications of various policy choices, a tactic that many interests have used in the Pacific salmon crisis (Taylor, 1999a). Such approaches only perpetuate conflict because, as we have seen in fishery after fishery in North America and Europe, any policy not reached through the messy, compromise-laden process of consensus building quickly migrates to the courts. Many of the problems attending salmonid hatcheries can only be resolved through political negotiation, and a prerequisite to a stable outcome will be an understanding of the historical development of those hatchery programmes. We must first step back and examine the historical lessons of these technologies before we can move intelligibly into the future.

4. GEOGRAPHICAL EXTENT OF ACTIVITIES

Here, we report on the numbers of salmon released from conservation and fishery enhancement hatcheries in the northern Atlantic and Pacific oceans. This section is intended to provide an understanding of the relative numbers of fish released in different regions, and to identify the main purposes for their releases.

4.1. Enhancement of indigenous salmonids: Conservation, production and mitigation hatcheries

4.1.1. Atlantic salmon (*S. salar*)

Atlantic salmon have been artificially propagated and released into the wild on a large scale for more than a century. While the goals of Atlantic salmon hatcheries are as varied as Pacific salmon hatcheries (e.g., supplementation of at-risk populations, compensation for human-mediated loss of production, reestablishment of extinct populations, and increased catch), Atlantic salmon hatcheries differ in several ways from those in the Pacific. Most obviously, hatchery operations in the Atlantic are based on a few species compared to the seven species propagated in Pacific hatcheries. The scale of hatchery operations also differs dramatically. For instance, the number of Atlantic salmon smolts released is about two orders of magnitude less than releases of coho and Chinook smolts in the Pacific (Isaksson, 1988). Atlantic salmon hatcheries frequently employ a ‘delayed release’ technique in which out-migrating juveniles are released directly into marine waters rather than rivers (Salminen *et al.*, 1995). While this practise appears to improve survival, it may increase straying (Gunnerød *et al.*, 1988).

4.1.1.1. Western Atlantic The United States releases Atlantic salmon in an effort to recover populations that have been extirpated or severely depleted for decades. Over the last 10 years, annual releases from hatcheries in the United States have averaged greater than 10 million (M), with a maximum 15.3 M in 2000 (Fig. 2.1). The vast majority of fish releases are fry (Fig. 2.2). An analysis has shown that of the nearly 193 M salmon released in New England since 1969 (Fig. 2.2), 79% were fry, 12.4% were smolts and 8.5% were parr (US Atlantic Salmon Assessment Committee, 2003). Additionally, adult salmon that were spent, or were excess to hatchery broodstock needs, have been released into US rivers, although these numbers are low

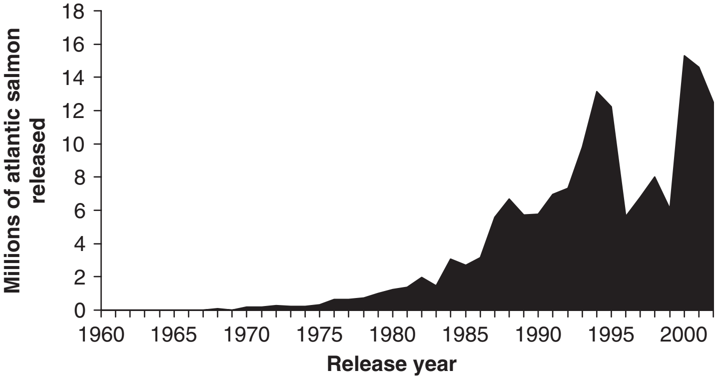

Figure 2.1 Number, in millions, of Atlantic salmon (*S. salar*) released from hatcheries into New England waters from 1960 to 2000 (all life stages). Data are from the US Atlantic Salmon Assessment Committee (2003).

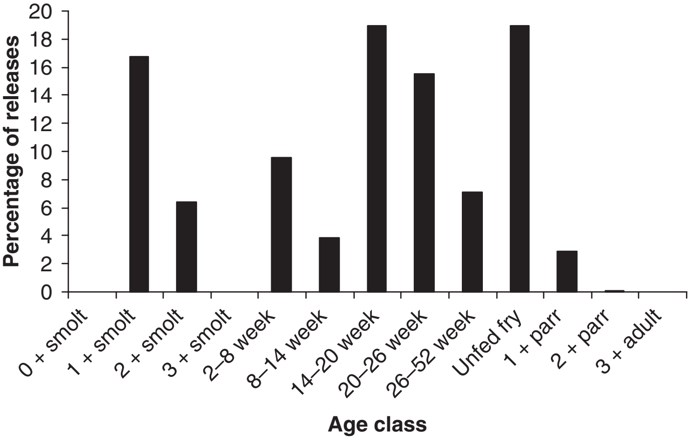

Figure 2.2 Percentage of Atlantic salmon (*S. salar*) released into New England waters by age class. Data are from the US Atlantic Salmon Assessment Committee (2003).

(e.g., 3576 in 2002). Twenty river systems have routinely received hatchery Atlantic salmon, but three of these rivers (Merrimack, Connecticut and Penobscot) account for more than 80% of total releases.

Despite the many millions of hatchery fry released over the last several decades, 88% of Atlantic salmon returning to US waters originated as hatchery smolts. The remaining 12% of returning fish originated from either natural spawning fish or hatchery fry. In general, however, return rates of hatchery fish have been very low. In 2000, for instance, the return rate of hatchery smolts released in the Penobscot River was 0.10% (US Atlantic Salmon Assessment Committee, 2003).

Canadian Atlantic salmon hatcheries have been built primarily to compensate for the loss or degradation of freshwater habitat as a consequence of hydropower development or other human activities. As with US releases, returns from Canadian smolt releases have been low, ostensibly as a result of harvesting in the Greenlandic fishery (Isaksson, 1988). From 1976 to 2002 nearly 80 M Atlantic salmon were released from hatcheries in the Canadian Maritimes. Of these, most fish released were unfed or young fry, while nearly 17% were 1+ smolts (Fig. 2.3).

4.1.1.2. ***Eastern Atlantic*** While Scotland, Ireland and Norway are the major worldwide producers of Atlantic salmon in commercial programmes, production of salmon reared in conservation or fishery enhancement hatcheries is small.

Legislation in Scotland governing the use of freshwater habitats limits the development of hatcheries in these environments (Thorpe, 1980). Nevertheless, about 14 M fish are released annually throughout the region, most of which comprise eyed ova, unfed and fed fry (B. Davidson, Association of Salmon Fishery Boards/Institute of Fisheries Management, personal communication). Approximately 15% are released as parr. The majority of fish released in these waters provide harvest opportunities, although some are released to compensate for habitat lost to hydroelectric power schemes. The region has seen better recovery following habitat restoration, and is turning to this approach as the primary conservation measure.

Production of juvenile salmon from Irish hatcheries is also modest relative to other countries. Unfed fry comprise the vast bulk of releases from hatcheries. Approximately 2.9 M fish were released in 2002. Releases of parr also take place, with 598,000 released in 2002 compared to 349,000 in 1999. About half a million smolts have been released each year since 1995

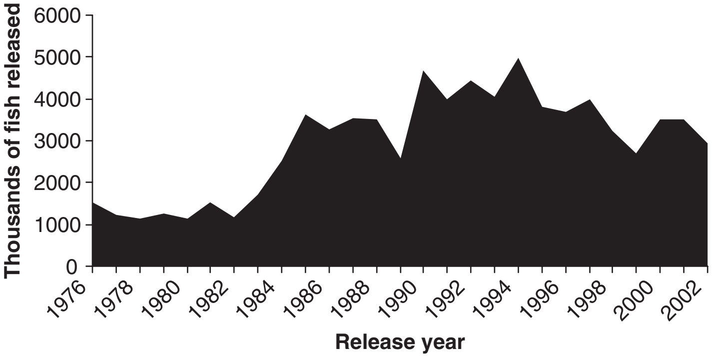

Figure 2.3 Number, in thousands, of Atlantic salmon (*S. salar*) (all life stages) released from hatcheries into waters of the Canadian Maritime provinces (Novo Scotia, New Brunswick, and Prince Edward Island) from 1976 to 2002.

(WGNAS, 2003). The major goal of these hatcheries is the preservation of fisheries which are affected by hydroelectric development (Isaksson, 1988).

In England and Wales, releases of Atlantic salmon are modest (Fig. 2.4). Currently (2000–2004), 1.4 M salmon are released annually, of which 42% are parr and smolts (Fig. 2.5). This release size contrasts with historical releases of 4.4 M in 1965–1969 and 3.0 M in 1987–1991 (N. Milner, Environment Agency, UK, personal communication). Hatchery releases in this region are intended to recover salmon stocks that declined as a result of poor estuarine water quality and loss of spawning and rearing habitat (Milner *et al.*, 2004).

In Norway, several hatcheries release Atlantic salmon in an effort to compensate for loss of spawning and juvenile rearing areas due to hydropower development. As with other East Atlantic countries, there was a rapid expansion of hatchery production in the 1980s, with recent annual releases of 8–9 M fry (Jonsson *et al.*, 1993). Even so, production of adult salmon from hatchery releases in Norway is small relative to other countries in the region.

Iceland is in a somewhat unique position relative to other countries in the Atlantic because salmon harvest is limited to terminal fisheries in streams (Isaksson, 1988). Iceland's hatchery programme began with experimental smolt releases in 1964 (Isaksson *et al.*, 1997; Fig. 2.6). After achieving return rates of 4–9% over the following 15 years (Isaksson, 1988), commercial releases began with the goal of supplying a privately owned terminal fishery. After a period of low return rates in the 1990s, commercial operations ended;

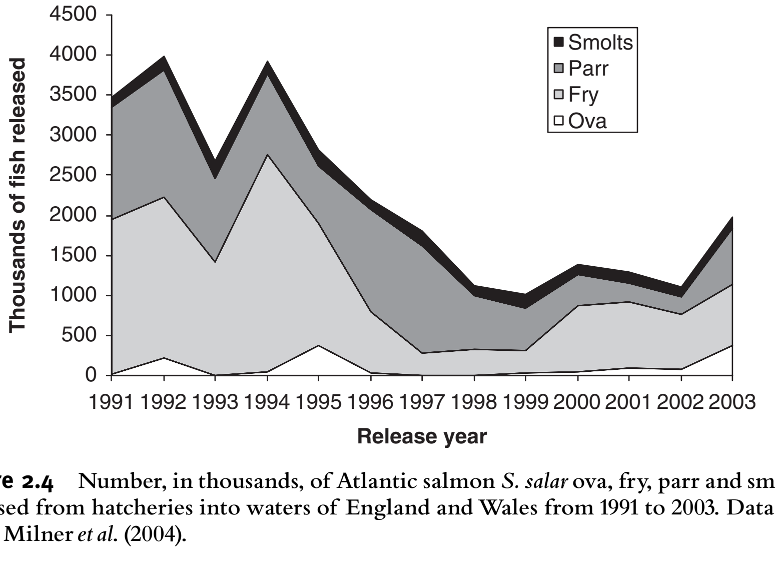

Figure 2.4 Number, in thousands, of Atlantic salmon *S. salar* ova, fry, parr and smolts released from hatcheries into waters of England and Wales from 1991 to 2003. Data are from Milner *et al.* (2004).

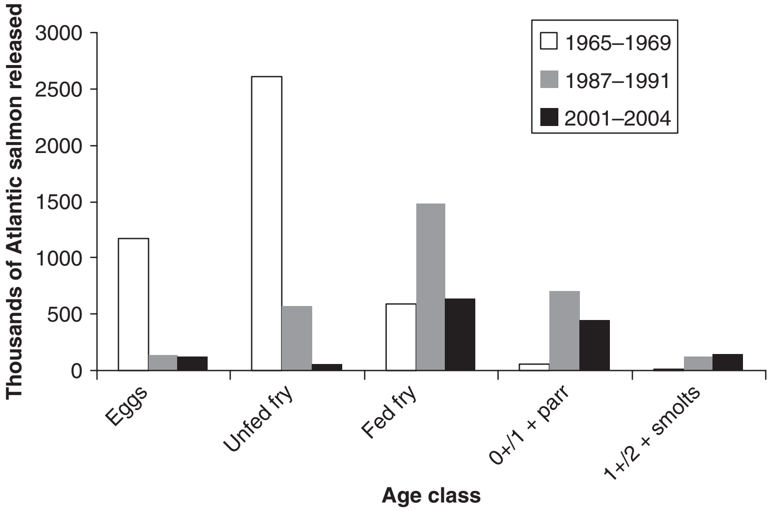

Figure 2.5 Number, in thousands, of Atlantic salmon (*S. salar*) released into waters of England and Wales by age class. Data are from Milner *et al.* (2004).

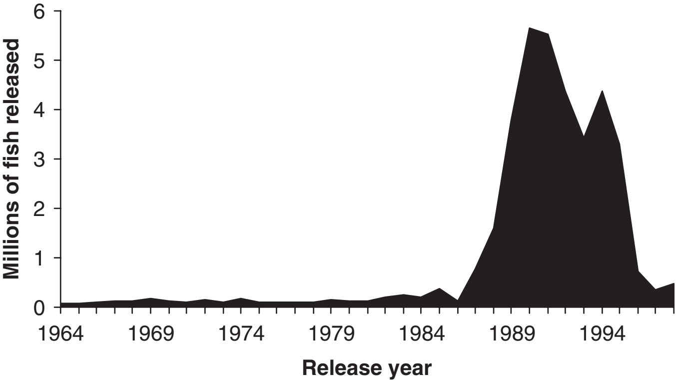

Figure 2.6 Number, in millions, of Atlantic salmon (*S. salar*) smolts released into Icelandic waters. Data redrawn from Isaksson *et al.* (1997).

however, there is still ongoing enhancement to increase abundance for angling (Isaksson and Oskarsson, 2002).

4.1.1.3. ***Baltic Sea*** Since the early 1950s, several extensive hatchery programmes have been in place throughout the Baltic Sea region with the aim of preserving and maintaining fisheries for Atlantic salmon stocks that have been drastically reduced by hydropower development and other forms of habitat degradation (Eriksson and Eriksson, 1993; Salminen and Erkamo, 1998). Specifically, countries surrounding the Baltic Sea have developed a

'Salmon Action Plan' (ICES, 2005), which aims to restore healthy runs of Atlantic salmon and sea trout. A number of rivers in Finland, Sweden, Estonia, Latvia, Lithuania and Russia have been identified for population restoration efforts (including hatchery intervention), with the eventual goal of creating self-sustaining populations of both species.

By the mid-1980s, natural production of Atlantic salmon had been largely replaced by artificial propagation throughout the Baltic [Eskelinen and Eriksson (1987) cited in Isaksson (1988)]. For instance, in 2001 total smolt production for the Baltic region was 7.9 M Atlantic salmon, of which 6.6 M (83.5%) were of hatchery origin (ICES, 2002). However, the proportion of hatchery-reared fish varies substantially among regions, with the proportion of hatchery-reared smolts as high as 98.4% in the Gulf of Finland (ICES, 2002).

Sweden began releasing hatchery fish during the 1950s and over the next decade the number of released smolts increased to about 1.5 M (Fig. 2.7). By the middle of the 1980s Swedish hatchery production increased to about 2 M (mainly 2-year-old) smolts. In the early 1970s, Finland began a smolt release programme that grew rapidly in the 1980s. In recent years, Finland has released nearly 2.5 M smolts into the Baltic (Fig. 2.7; ICES, 2005).

A number of other Baltic countries have hatchery programmes, and their contribution to regional hatchery production increased in the late 1980s. In 2001, in addition to Sweden and Finland, Poland, Latvia, Estonia and Russia released salmon into the Baltic (Fig. 2.8). Denmark and members of

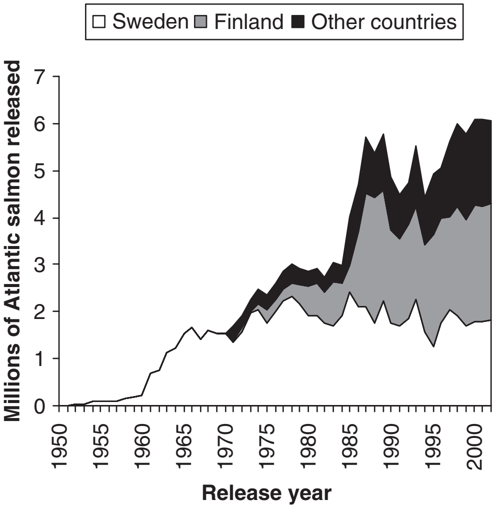

Figure 2.7 Number, in millions, of hatchery-raised Atlantic salmon (*S. salar*) smolts released into the Baltic Sea. Data extracted from Eriksson and Eriksson (1993) and ICES (2002).

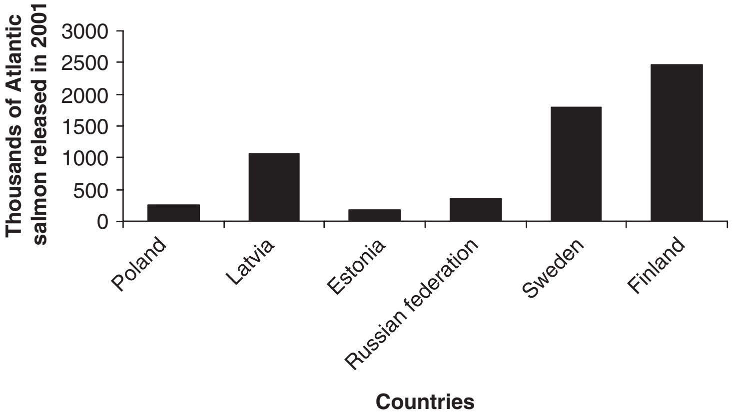

Figure 2.8 Number of hatchery-raised Atlantic salmon (*S. salar*) smolts released by country into the Baltic Sea. Data from ICES (2002).

the European Union also released small numbers of salmon in the 1990s (ICES, 2002). Mixed-stock analysis using genetic approaches have shown that hatchery fish comprise 20–75% of the total Finnish catch, depending on the region harvested (ICES, 2005).

4.1.2. Sea trout (*S. trutta*)

Sea trout the anadromous form of *S. trutta* are subject to hatchery production, but this is small in most countries. There are two exceptions.

The Baltic Sea countries release sea trout to compensate for spawning habitat lost through anthropogenic activities such as pollution, harvest, damming and dredging. The majority of hatchery fish support fisheries, although a few are used to rehabilitate threatened or extirpated populations (ICES, 2005). All early life history stages (to 2-year-old smolts) are released. Hatchery production has been fairly constant since 1988 (Fig. 2.9); Sweden, Poland and Finland are the greatest contributors of hatchery fish to the Baltic Sea. Finland and Estonia release about half of their smolt production directly to the coastline, while the remaining fish are released in dammed rivers. The majority of countries collect broodstock from naturally returning fish, but Poland's production relies almost entirely on hatchery fish; the wild populations are believed to be very small in this country (ICES, 2005).

In Ireland sea trout fisheries were, before the late 1980s, very important sport fisheries, but they collapsed dramatically due to the impacts of sea lice infection associated with marine salmon farming (Whelan and Poole, 1996). Similar decline occurred in Scottish west coast sea trout fisheries, also linked to salmon farming.

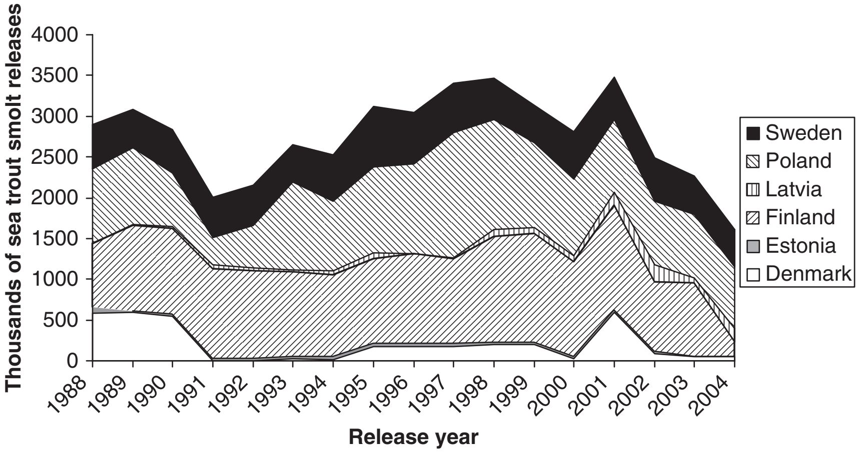

Figure 2.9 Number of hatchery-raised anadromous sea trout (*S. trutta*) smolts released into the Baltic Sea by country from 1988 to 2004. Russia and Lithuania released small numbers in the early years of this time series but are not included here. Data from ICES (2005).

4.1.3. Pacific salmon (*Oncorhynchus* spp.)

Salmon hatcheries in the Pacific date from the 1870s, when the US Fish Commision established a hatchery on the McCloud River in California (Lichatowich, 1999). Early hatcheries were directed towards the enhancement of depleted stocks or mitigation for habitat loss, but these hatcheries achieved limited success because nearly all operations relied on releases of young fry that had low survival rates (Mahnken *et al.*, 1998). Important innovations in feeding technology, disease control and rearing early life history stages occurred in the 1950s and 1960s leading to releases of larger fish with higher survival rates (Lichatowich and McIntyre, 1987), and since this time, hatcheries have played a major role in the management of Pacific Rim salmonids.

4.1.3.1. British Columbia Hatcheries have existed in British Columbia since the first sockeye (*O. nerka*) hatchery began production in the 1890s. These early hatcheries were substantial, with total output in 1910 around 500 M fish (Peterson *et al.*, 2002), more than the current production in British Columbia (Fig. 2.10). Hatchery production ceased after a couple of decades because it was difficult to demonstrate any increase in production as a result of artificial propagation (Section 2; Wood *et al.*, 2002), but began again in the 1960s (Section 2). In 1977, the Salmon Enhancement Programme (SEP) of Canada was started with the aim of doubling the catch of Pacific salmonids by protecting, rehabilitating and enhancing fish stocks throughout British Columbia. Artificial propagation has played a major role in the hatcheries formed under the SEP; spawning and rearing

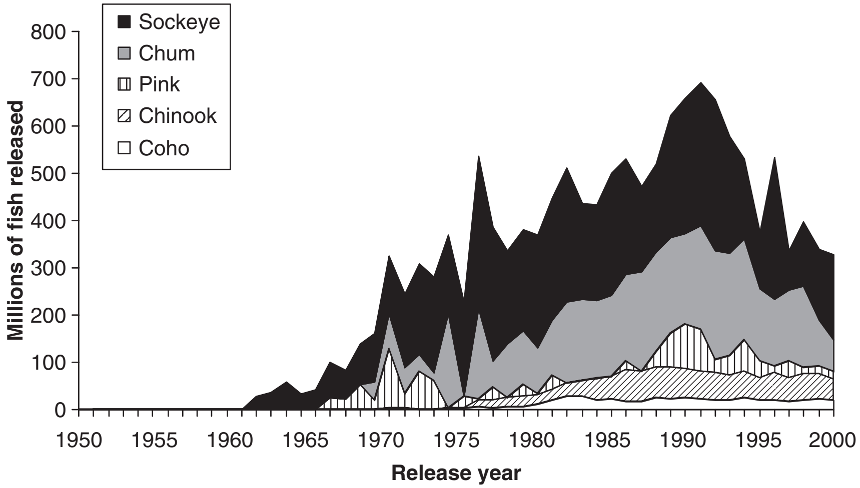

Figure 2.10 Number of hatchery fish by species (all life stages) released from British Columbia hatcheries and spawning channels. Included are sockeye (*O. nerka*), chum (*O. keta*), pink (*O. gorbuscha*), Chinook (*O. tshawytscha*) and coho (*O. kisutch*) salmon. Data from the North Pacific Anadromous Fish Commission (http://www.npafc.org/).

channels and in-stream incubation boxes are intended to speed the recovery of depleted stocks. British Columbia currently has 38 federally operated hatcheries and an additional 150 public involvement projects (e.g., classroom hatcheries or classroom incubators; Wood *et al.*, 2002).

Production from British Columbia hatcheries and spawning channels peaked in 1992 when nearly 700 M fish were released (Fig. 2.10). Since then production has declined, with recent releases totalling around 330 M fish. Throughout the time series examined here, sockeye and chum (*O. keta*) have dominated hatchery and spawning channel production, with sockeye comprising 41% (mostly spawning channel production) and chum 34% of production in recent years. Additionally, an average of 20 M coho, 53 M Chinook (*O. tshawytscha*) and 41 M pink salmon (*O. gorbuscha*) have been released in recent years [Fig. 2.10; North Pacific Anadromous Fish Commission (http://www.npafc.org/)].

4.1.3.2. Japan Japan operates the most extensive hatchery operation in the world, with the goal of supporting its salmon fisheries. Japanese hatchery programmes date from 1888, when the Chitose River Central Hatchery was built in Hokkaido (Johnson *et al.*, 1997). Within 12 years, 45 chum salmon hatcheries were constructed. However, as in other regions of the Pacific Rim, fish culture practises were not well developed and the majority of releases comprised unfed fry. Beginning in the 1960s, improvements in feeding led to an increase in the size of juveniles, and as the percentage of fed fry increased, return rates to hatcheries also increased substantially, reaching 2.3% after 1966 (Isaksson, 1988; Mahnken *et al.*, 1998).

Currently more than 300 chum salmon hatcheries are located on the islands of Honshu and Hokkaido, and at least 262 rivers are managed almost entirely for artificial propagation. Over 2 billion salmon are released annually from these hatcheries. Chum salmon have made up about 93% of recent releases (Fig. 2.11). Additionally, an average of about 132 M pink and 15 M masu salmon (*O. masou*) have been released annually into Japanese waters over the last decade (North Pacific Anadromous Fish Commission, http://www.npafc.org/).

4.1.3.3. ***Russia*** The first salmon hatcheries in Russia began production in the 1920s in tributaries to the Amur and Kamchatka rivers. At this time, the Japanese also built hatcheries on Sakhalin Island and the Kuril Islands, which came under Russian control after World War II (Johnson *et al.*, 1997). By the 1960s, 25 hatcheries operated in Russia and recently 44 hatcheries have produced 500–550 M salmon annually in an effort to enhance fisheries (Environment and Natural Resources Institute, 2001). Production is almost entirely based on chum and pink salmon and is approximately evenly distributed between the two species (Fig. 2.12). In addition, close to 3 M coho, 5 M sockeye, 400,000 Chinook and 200,000 masu have been released annually (Environment and Natural Resources Institute, 2001).

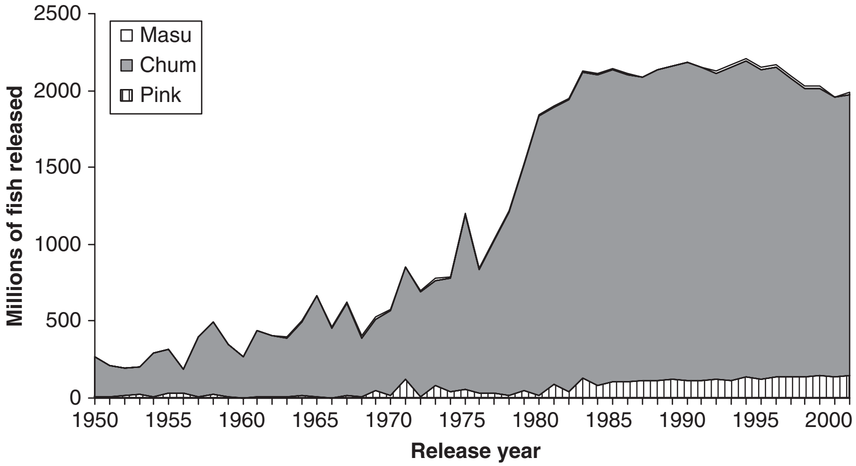

Figure 2.11 Number, in millions, of hatchery fish by species (all life stages) released from Japanese hatcheries from 1950 to 2000. Included are masu (*O. masou*), chum (*O. keta*) and pink (*O. gorbuscha*) salmon. Data from the North Pacific Anadromous Fish Commission (http://www.npafc.org/).

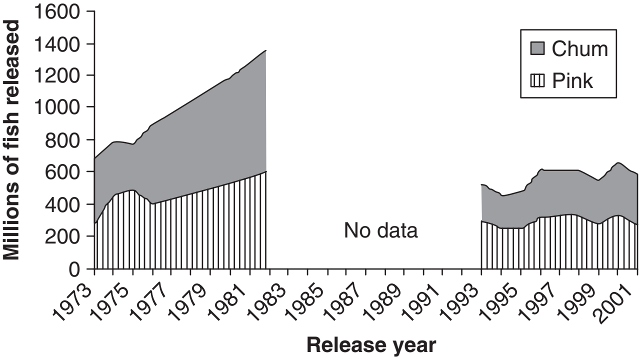

Figure 2.12 Number of hatchery chum (*O. keta*) and pink (*O. gorbuscha*) salmon (all life stages) released from Russian hatcheries from 1973 to 2001. Sockeye, masu, chinook and coho are not included; see text for numbers released during this period.

Russian hatcheries differ from Japanese programmes in that they were not constructed to manage rivers exclusively for hatchery fish. Consequently, Russian hatcheries generally have used local fish for broodstock and there is no attempt to prevent natural spawning. Even so, natural production was not afforded a high priority as, historically, eggs were widely exchanged among hatcheries and excess hatchery fish were allowed to spawn with wild fish. In recent years, however, hatchery managers have recognized the problems associated with egg transfers and such exchanges have been reduced (Johnson *et al.*, 1997).

4.1.3.4. ***Alaska*** Construction of hatcheries in Alaska began in the early 1900s, but they were often badly sited and had poor water quality. As a consequence, these hatcheries achieved little success and by 1936 Alaska's hatcheries ceased production (Roppel, 1982). However, after a protracted decline in salmon catches in the early 1970s, the Alaska Department of Fish and Game developed a coordinated SEP and the state of Alaska passed legislation that encouraged 'PNP' hatcheries. Over the next several years, there was an explosion of hatchery construction (Fig. 2.13; Farrington, 2003) and corresponding hatchery releases (Fig. 2.14). A unique feature of Alaska's hatchery system is that most hatcheries are operated by private associations of fishers, environmentalists and local civic interests (Heard *et al.*, 2003). These associations can not only build and operate hatcheries, but they also assist the Alaska Department of Fish and Game in the development of regional salmon plans, authorize taxes on salmon catches to support hatcheries and sell returning hatchery fish to offset operational expenses (Heard *et al.*, 2003). Currently, there are eight regional aquaculture associations in Alaska.

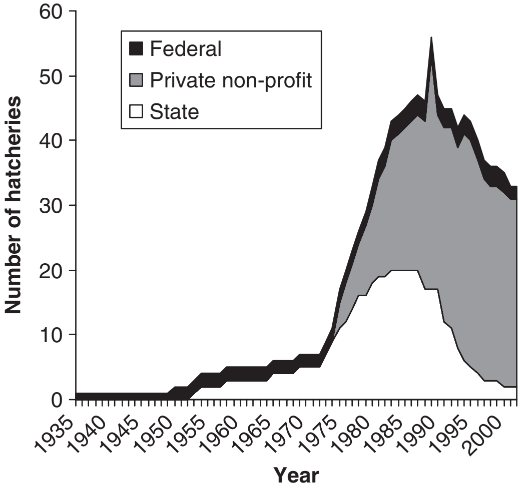

Figure 2.13 Number of federal, state and private Pacific salmon (*Oncorhynchus* spp.) hatcheries operating in Alaska (Farrington, 2003).

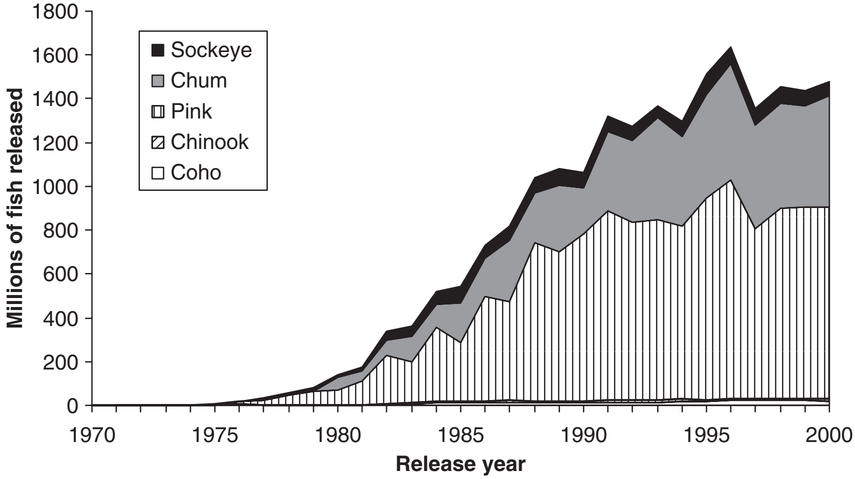

Figure 2.14 Number, in millions, of hatchery salmon by species (all life stages) released from Alaska hatcheries. Data from the North Pacific Anadromous Fish Commission, 2003 (http://www.npafc.org/). Included are sockeye (*O. nerka*), chum (*O. keta*), pink (*O. gorbuscha*), Chinook (*O. tshawytscha*) and coho (*O. kisutch*) salmon.

Pink and chum salmon have made up the bulk of the salmon produced in Alaska hatcheries (Fig. 2.14). In recent years, more than 1.4 billion salmon have been released annually; 61% are pink and 32% are chum, respectively. In addition, recent annual sockeye releases have averaged more than 70 M (5%), coho releases have averaged about 18 M (1.3%)

and Chinook releases have averaged nearly 9 M (0.6%). The PWS and Southeast Alaska regions are the largest producers of hatchery salmon. The Prince William Sound Aquaculture Corporation releases more than 400 M pink salmon each year and operates the largest hatchery operation in North America (Environment and Natural Resources Institute, 2001).

Hatchery-produced fish appear to contribute significantly to harvest levels in Alaska. In 2000, hatchery fish comprised 42% of Alaska's pink, 64% of chum, 19% of Chinook, 24% of coho and 4% of sockeye catches (Heard *et al.*, 2003). However, the proportion of hatchery fish in the catch varied greatly among regions. For instance, 82% of the pink and 88% of the chum harvest in PWS was of hatchery origin. In contrast, hatchery fish comprised only 10% of the total salmon harvest (2% pink, 0% chum) in Cook Inlet (Heard *et al.*, 2003).

4.1.3.5. United States, Contiguous Pacific States Salmon hatcheries in the US Pacific Northwest have played an increasingly prominent role in salmon management. Most public hatcheries were originally constructed to rebuild depleted stocks and to mitigate for loss of natural spawning habitat, and their goal was simply focused on enhancing the harvest of adults in the commercial fisheries (Flagg *et al.*, 2000). The number of hatcheries increased gradually throughout the first half of the twentieth century; facilities were constructed at a rate of about 1.5 per year from 1900 until 1950. However, the pace of construction increased rapidly in the latter part of the century, at a rate of nearly 6 per year from 1951 to 2000.

Total hatchery production peaked in the early 1980s with the release of nearly 600 M salmon (Fig. 2.15). More recently, total annual hatchery releases have averaged about 400 M. Chinook salmon dominate the releases in the Pacific Northwest with average annual releases of 256 M fish from 1990 to 2000. The centre of Chinook production is the Columbia River Basin, which accounts for about 27% of the world's total Chinook release (Mahnken *et al.*, 1998). Coho and chum are also produced in large numbers, with annual average releases from 1990 to 2000 of 77 and 66 M fish, respectively. Additionally, hatcheries in the region annually release steelhead (*O. mykiss*; 28 M per year), sockeye (11.6 M per year) and pink salmon (1.8 M per year). Interestingly, hatchery releases do not correspond directly to the number of hatcheries constructed (Fig. 2.16). For Chinook, for example, there appears to be a step function, with average annual production increasing abruptly in the 1950s and subsequently varying around a greater mean than in previous years (Fig. 2.16).

While salmon hatcheries operate in California, Idaho, Oregon and Washington, the majority of hatchery fish are produced in Washington. In 1998, more than 70% of Pacific salmon released in the mainland United States originated from Washington hatcheries, with 16% from California, 10.4%

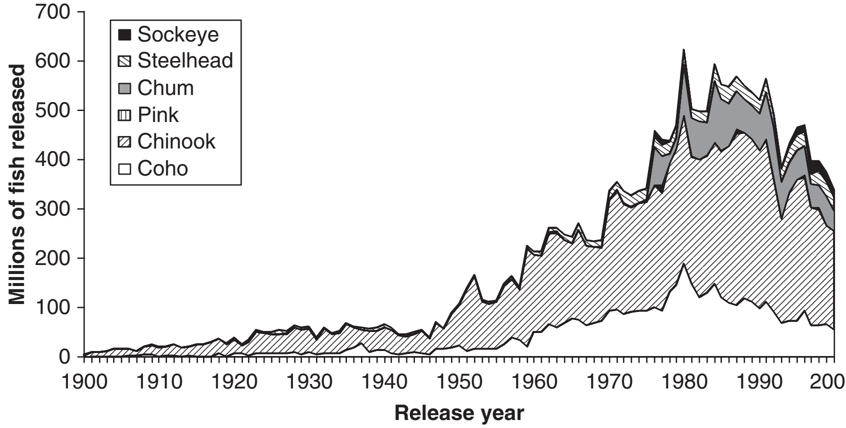

Figure 2.15 Number, in millions, of hatchery Pacific salmon (*Oncorhynchus* spp.) (all life stages) released from hatcheries in the continental United States. Data from the North Pacific Anadromous Fish Commission (http://www.npafc.org/) and Mahnken *et al.* (1998). Included are sockeye (*O. nerka*), chum (*O. keta*), pink (*O. gorbuscha*), Chinook (*O. tshawytscha*) and coho (*O. kisutch*) salmon.

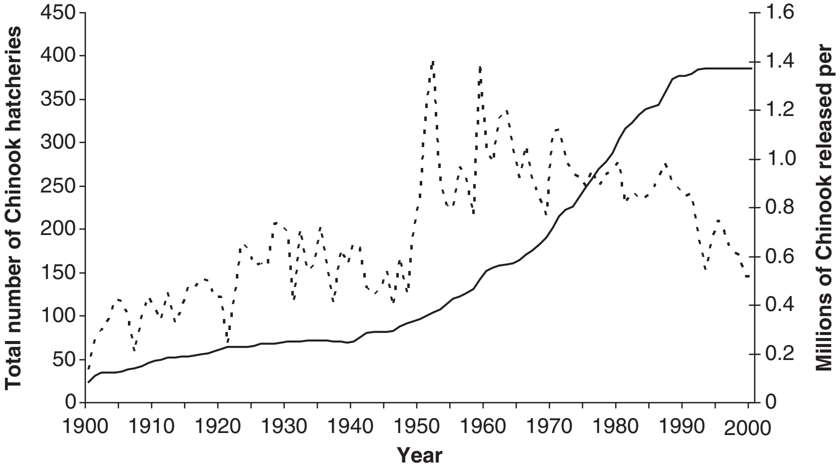

Figure 2.16 Cumulative number of Chinook salmon hatcheries (solid line) and the average number of hatchery Chinook salmon *O. tshawytscha* (dashed line) released into continental US water per hatchery from 1900 to 2000. Data extracted from Myers *et al.* (1998) and the North Pacific Anadromous Fish Commission (http://www.npafc.org/).

from Oregon and 2.7% from Idaho (North Pacific Anadromous Fisheries Commission Statistical Yearbook, available at http://www.npafc.org/).

As part of the management process in the Pacific Northwest, hatcheries are required to state the purpose of their operations (Drake *et al.*, 2003). We grouped these operational goals into three of the categories outlined earlier

(Section 1.2): mitigation, supplementation or production hatcheries. The purpose of hatcheries varied greatly among species (Fig. 2.17). The stated purpose of most coho and steelhead hatcheries, for example, was production, while conservation was the primary purpose of most chum hatcheries.

Drake *et al.* (2003) also reviewed available published literature and unpublished studies and subjectively classified hatchery stocks based on the amount of genetic divergence between the hatchery and wild stocks and the source of the hatchery stock relative to wild stock. The hatchery fish were classified as local or non-local, and if the latter, as within or outside evolutionary significant units (ESUs; Waples, 1995).

The source of most Chinook stocks was found to be local or non-local but within the ESU (Fig. 2.18). In general, Drake *et al.* (2003) determined that while there were moderate to few wild fish in most Chinook hatchery broodstock, there was no more than moderate divergence of the hatchery stocks from the wild fish. Additionally, the ratio of hatchery Chinook to the natural population was high for a number of stocks. This result meant that there were substantial numbers of natural origin fish in the Chinook broodstock and there was minimal divergence between hatchery and wild fish. A minority of hatchery stocks comprised broodstock whose source was outside the ESU, and in these stocks, there was extreme divergence between hatchery and wild fish. A similar pattern emerged for steelhead; many hatchery stocks exhibited little divergence from natural populations, but a significant number of stocks showed substantial or extreme divergence (Fig. 2.18). This latter result may be partly explained by the use of a deliberately domesticated hatchery stock with a different return timing from wild populations. Coho hatchery stocks generally had no more than moderate divergence from wild stocks, and chum hatchery stocks showed little divergence from fish of natural origin.

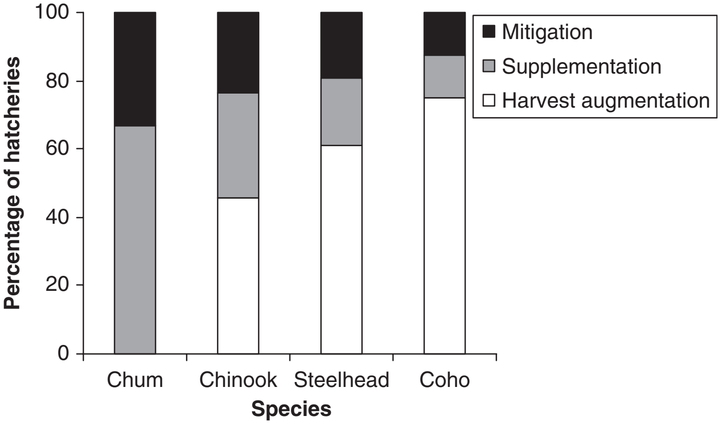

Figure 2.17 Declared purpose of hatcheries for each of four species of Pacific salmon in the Pacific Northwest. Data are from Drake *et al.* (2003).

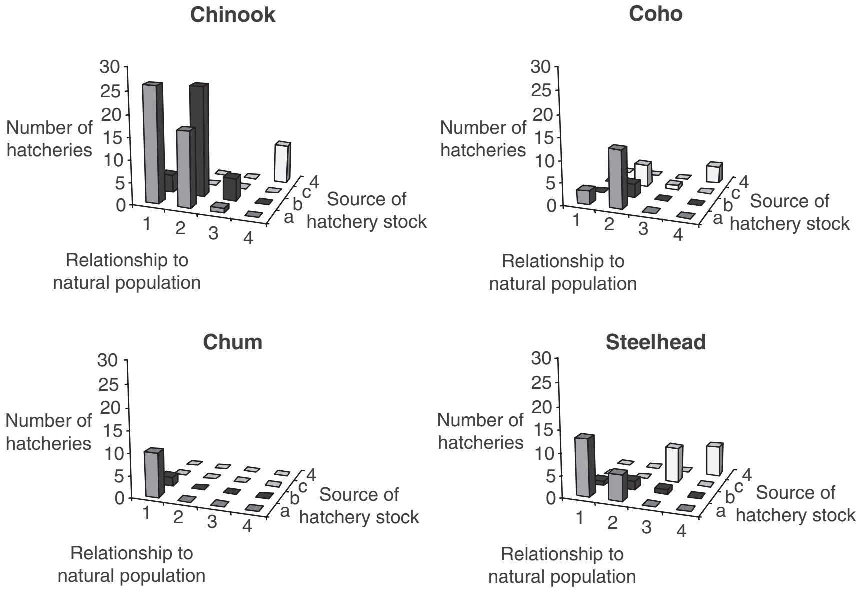

Figure 2.18 Number of steelhead (*O. mykiss*), Chinook (*O. tshawytscha*), coho (*O. kisutch*) and chum (*O. keta*) salmon hatcheries organized by the amount of genetic divergence between the hatchery and wild stocks (relationship to natural population) on a scale of 1–4, and the source of the hatchery stock relative to wild stock (source of hatchery stock) on a scale of a–c for stocks within an ESU, and 4 for those outside an ESU. Data are from Drake *et al.* (2003).

4.2. Enhancement of non-indigenous salmon and trout: Introductions

The literature on worldwide salmon and trout introductions is extensive, and will be reviewed elsewhere. Several general conclusions relevant to our discussion can be drawn from these findings. First, data on release sizes for anadromous salmonids in conservation, production and mitigation hatcheries were not readily obtained (Section 4.1), and similar data on introductions were not available in most cases. In addition, it appears difficult to discriminate between those introductions that were successful versus those that were not. Second, there were inconsistencies in the scales over which the data were reported, and these scales varied historically. Third, it appears that the extent of introductions worldwide has declined, possibly because most potential sites for salmon fisheries have been explored. However, there is a paucity of data on ongoing ‘put and take’ hatcheries based on non-indigenous salmon, and it is difficult to gauge the level, extent and impact of these activities. Finally, the ongoing tension between economic and ecological incentives is identified as being a primary determining force as to whether exotic introductions will continue. We do not explicitly address the consequences of non-indigenous salmon introductions in most of the risks that we review. However, the introduction of exotic salmon may result in extreme outcomes of these risks; for example, competition with local species, the introduction of a non-endemic pathogen or hybridization with vulnerable indigenous species.

5. POTENTIAL CONSEQUENCES OF ENHANCEMENT ACTIVITIES

5.1. Genetic risks associated with salmon hatchery programmes

The genetic effects of hatchery programmes have been the subject of substantial review in the literature. Most authors agree that releases can have detrimental effects on wild populations (e.g., Allendorf and Ryman, 1997; Aprahamian *et al.*, 2003; Busack and Currens, 1995; Cross, 2000; Hindar *et al.*, 1991; Utter, 1998; Waples, 1991) and others have suggested management steps that may be taken to reduce such effects (Hard *et al.*, 1992; Mobrand *et al.*, 2005; Waples and Drake, 2005). The debate in this area is not around whether hatchery programmes pose a threat to wild populations, but whether the risks are sufficiently large to compromise wild populations and if true, whether they may be reduced or avoided through correct management actions (Brannon *et al.*, 2004a; Campton, 1995; Waples, 1999).

The aim of this section of the chapter is not to simply repeat the information provided in many of the papers written on this topic, but to update and evaluate our understanding of the genetic consequences of hatchery programmes. First, we will review the current knowledge of the genetic risks involved. Second, most would argue that the varying objectives of hatchery programmes will pose different types and magnitudes of effects on wild populations, and so we will examine the impacts of hatchery programmes in the context of their release objectives (conservation or fishery enhancement hatcheries, following the classification outlined in Section 1). Finally, we will identify research directions that will assist designing management steps that may be taken to reduce the genetic risks associated with different salmon hatchery programmes.

5.1.1. Genetic risks associated with hatchery fish

The potential genetic outcomes of rearing and releasing hatchery fish into the wild fall broadly into three categories: the effect of hatcheries on hatchery fish, the direct effect of hatchery fish on wild fish and the indirect effect of hatchery fish on wild fish (Campton, 1995; Hindar *et al.*, 1991;

Waples, 1991). The latter occurs through processes such as competition, disease transfer and increased fishing mortality on the wild component of a stock, all of which result in demographic changes or selection in the wild populations. The first two factors will be reviewed in detail below, primarily because much is known about these factors, while the third has not been empirically studied to any significant extent (Campton, 1995; Waples, 1991), and so will not be discussed further in this section.

5.1.1.1. The genetic effects of hatcheries on hatchery fish Procedures implemented in the collection, mating, rearing and release of hatchery salmon may lead to a change and perhaps a reduction in genetic diversity of the source population in two ways. First, as the population size decreases, the random loss of genetic variation in a population can be expected to increase. A loss of genetic variation may lead to inbreeding and an associated decrease in fitness, termed inbreeding depression. Second, the hatchery environment can be a poor imitator of wild conditions, and hatchery fish may become adapted to their environment through a process known as domestication selection. The result of both effects may ultimately lead to the release of a genetically altered population that may interact negatively with any wild stocks present, by decreasing the overall fitness of the combined populations.

5.1.1.1.1. Loss of genetic diversity and inbreeding The genetic diversity relevant to the long-term survival of a species is quantitative in nature, that is, several gene loci interact with each other and with the environment to create a range of phenotypes. Quantitative genetic diversity is difficult to measure at present (Hard, 1995), although substantial advances are being made in characterizing this functional diversity (reviewed in Danzmann and Gharbi, 2001; Vasemägi and Primmer, 2005). Thus, effective population size is often used as a proxy metric for quantitative genetic diversity because the theoretical link between this measure and loss of genetic variation is well known (Frankham *et al.*, 2002).

The effective population size, N_e, is the size of an ideal population whose genetic composition is influenced by random processes in the same way as a real population. It is important to realize that N_e can be very different from the census size, N_c, of a population, and the ratio of N_e to N_c can be affected by factors such as sex ratio, family size, fluctuations in population size, overlapping generations and variance in reproductive success. The measurement of N_e in salmon populations is usually confounded by overlapping generations, seen in most species; hence N_b, the number of breeders corrected for generation length, is often the preferred measure (Waples, 1990, 2004). The ratio of N_b (or N_e) to N_c in wild salmon populations is often low (e.g., Shrimpton and Heath, 2003), and has been noted to vary between 0.01 and 0.71 (Bartley *et al.*, 1992; Hedrick *et al.*, 1995; Waples *et al.*, 1993).

A number of practises associated with the management of hatchery fish may lead to a decrease in N_e (Busack and Currens, 1995). For example, hatcheries may cause accelerated growth, which in turn may cause early maturation in male salmon and thus skew male to female ratios (Larsen *et al.*, 2004). Spawning protocols that deviate from 1:1 sex ratios are known to reduce N_e (e.g., Allendorf, 1993). Genetic variation may also be lost at the founding of the hatchery strain, during a bottleneck or during prolonged periods of reduced population size. Most studies have not examined the underlying causes of a decline in genetic diversity, but such decreases of diversity in hatchery strains have been reported at neutral genetic markers (Jones *et al.*, 1997; Koljonen *et al.*, 1999; Nielsen *et al.*, 1997; Primmer *et al.*, 1999; Tessier *et al.*, 1997; Was and Wenne, 2002). Where a decrease in N_e has been directly measured, it is often possible to attribute the decrease to broodstock practises that may be avoidable (Koljonen *et al.*, 2002).

On a positive note, it is widely recognized that if management steps are taken to avoid a loss of variation, then the N_e to N_c ratio within a captive population can be higher than that in the wild. For example, if founder population sizes are adequate (Allendorf and Ryman, 1997; Frankham *et al.,* 2002), sex ratios are equalized at mating (Campton, 2004), family sizes are also equalized (Allendorf, 1993) and long-term fluctuations in population sizes are avoided, then N_e to N_c ratios can exceed 1.0. Thus, captive populations may be used to enhance the genetic diversity in a depleted wild population (Hedrick *et al.*, 2000).

However, a loss of genetic variation may be unavoidable in some cases. The inevitable consequence is that a self-perpetuated broodstock will eventually comprise individuals with higher average relatedness, and mating between these individuals will result in inbreeding (identity by descent). Inbreeding by itself does not result in a change in gene frequencies; it does, however, result in an increase in homozygotes. Inbreeding is often associated with a decline in fitness-related phenotypes (Keller and Waller, 2002), termed inbreeding depression, which in turn may lead to a reduction in population size and a change in gene frequencies through genetic drift (Bijlsma *et al.*, 2000; Saccheri *et al.*, 1998). Inbreeding depression is usually more prevalent in life history traits than in morphological traits (DeRose and Roff, 1999) and tends to be more severe in wild than in captive populations (Crnokrak and Roff, 1999; Kalinowski and Hedrick, 1999).

The manifestation of inbreeding depression is usually attributed to one of two mechanisms, either the loss of dominance (‘masking’ of deleterious alleles) or of over-dominance (heterozygote advantage) at genetic loci encoding fitness traits (Frankham *et al.*, 2002). Deleterious alleles may increasingly occur in the homozygous state following inbreeding, thus reducing the dominance interactions between advantageous and deleterious alleles in heterozygotes. It has been argued that a fitness decline is controlled by the *rate* of inbreeding because deleterious alleles occur more frequently as homozygotes in small populations, and are no longer masked by positive or neutral dominant alleles. Selection can then act by 'purging' these alleles from the population. However, many researchers have demonstrated that selection against deleterious alleles cannot be relied on to decrease the rate of extinction because these alleles can also become fixed in a population through genetic drift (Reed *et al.*, 2003). An alternative explanation for a decline in fitness is attributed to the advantage conferred by over-dominance at heterozygous loci; that is, the sum of two alleles at a locus may outweigh either of the two homozygotes. If heterozygotes are lost, then overall fitness will decline in a population. If over-dominance is the underlying mechanism for inbreeding depression, then purging cannot be implemented as a management tool and in fact, the over-dominance hypothesis may partly explain why this approach is unpredictable in many cases.

Wang *et al.* (2002) provided several examples of inbreeding depression in their review of inbreeding in salmonids. Perhaps their most significant finding was that experimental designs have varied, and general inferences about the incidence and manifestation of inbreeding depression in the salmonids cannot easily be drawn. There are three major approaches to testing inbreeding depression in a population (Keller and Waller, 2002): (1) the experimental comparison of inbred with outbred lines, (2) the outcrossing of small inbred populations to examine whether an increase in heterozygosity results in an increase in fitness, and (3) the comparison of the phenotypic values of related versus unrelated individuals within a population. Inbreeding studies on salmonids have favoured the first method and have differed in the rates of inbreeding reported (Wang *et al.*, 2002). In a typical experiment using sexually reproducing organisms, inbred individuals are produced only after at least two generations of mating. Such experiments can be especially protracted in salmon, most of which reach maturity after several years. Hence, most studies have generated individuals with high inbreeding values as early as possible. Wang *et al.* (2002) proposed that the contradictory results seen by different researchers at the same traits and in the same species can be explained by the rates of inbreeding, most of which are not characteristic of wild populations. For example, Gjerde *et al.* (1983) reported inbreeding depression in adult body weight of rainbow trout *O. mykiss* under fast inbreeding, whereas Pante *et al.* (2001) do not observe this outcome under slower inbreeding. This contrast supports the notion that purging may play a role in avoiding fitness declines in salmonids, a view which needs to be verified by further research.

Other equally important factors may also affect the manifestation of inbreeding depression in the reported studies. For example, the initial inbreeding coefficient, F, of the baseline population may differ between experimental populations (Wang *et al.,* 2002), as may the prevailing environmental or social conditions (Gallardo and Neira, 2005). Inbreeding depression also varies by the trait measured (DeRose and Roff, 1999) and this trend certainly appears to be supported within salmonids. For example, early growth-related traits and survival appear to be more prone to inbreeding than adult weight and size (Wang *et al.*, 2002), and inbred Chinook salmon have been found to be more susceptible to the pathogen *Myxobolus cerebralis*, but not to *Listonella anguillarum* or infectious hematopoietic necrosis virus (IHNV; Arkush *et al.*, 2002).

Perhaps the most conspicuous point here is that the majority of such studies have been carried out on cultured fish. If the incidence of inbreeding depression in salmon increases in the wild, as in other taxa (Crnokrak and Roff, 1999; Kalinowski and Hedrick, 1999), then more emphasis on wild populations is needed. The design of such experiments should be systematic, include both resident and anadromous forms and populations with inbreeding history and those without. Such broadened studies likely will be more amenable to generalizations about the effects of inbreeding in systems incorporating hatchery releases.

5.1.1.1.2. Domestication selection Domestication selection that arises in a supplementation programme is often unintentional, resulting from 'natural' adaptation of the species to the hatchery. Simply, life history theory predicts that selection imposed by a novel environment will rapidly alter the genetic architecture of life history traits of a population, and lead to divergence between the founding and the new population. The strength of this change will be dependent on the selection regimes between the hatchery and the wild environment, the numbers of generations that the broodstock are held in captivity and the magnitude of genetic variation underlying the fitness trait under selection. Thus, the opportunity for domestication selection to produce divergence between wild and captively reared individuals is largest when the latter are cultured throughout their life histories for many generations (Hard, 1995). However, simulations have shown that domestication selection in hatchery fish can have rapid and substantial negative genetic effects on targeted wild populations, even when wild captive breeders are always used (Lynch and O'Hely, 2001; Ford, 2002).

Examples of differences between hatchery and wild fish are widely published. However, it should be noted that in many of these cases it is difficult to implicate domestication selection alone. For example, a series of experiments have demonstrated behavioural and morphological differences between wild populations and hatchery coho salmon (Fleming and Gross, 1992, 1993) and Atlantic salmon originating from aquaculture facilities (Fleming and Einum, 1997; Fleming *et al.*, 1994, 1996). While many of these experiments serve to demonstrate the rapid phenotypic divergences that may be obtained following deliberate domestication, the cultured strains used in some of these studies were not derived from the same watershed as the wild populations. In fact, Reisenbichler and Rubin (1999) pointed out that the prevalence of this experimental design in most studies, and the fact that many researchers examine only one or two fitness-related traits, has resulted in the charge that domestication selection has yet to be demonstrated in hatchery salmonids. On the west coast of North America, hatchery coho salmon have been compared to their wild source counterparts. Juvenile cultured coho salmon are less aggressive at emergence and adult hatchery fish are not as successful at mating as wild hatchery fish (Berejikian *et al.*, 1997, 1999, 2001a). The two groups also differ morphologically (Hard *et al.*, 2000). However, in an informative series of experiments, dissimilarities between hatchery and wild steelhead (*O. mykiss*) have been substantially reduced by rearing hatchery fish in enriched environments (Berejikian *et al.*, 2000, 2001b). Thus, an explanation for many of the variations observed between hatchery and wild fish is that the different rearing environments have acted to change the phenotypes without substantially changing the underlying genotype, thus confounding a genetic interpretation of the results of these studies. However, there are cases where the evidence indicates that a hatchery population diverged from the wild population from which it was derived (e.g., anti-predator and aggressive behaviour of juvenile steelhead trout Berejikian, 1995; Berejikian *et al.*, 1996). In addition, the adults selected for spawning in a hatchery are often the early arrivals, with the result that the distribution of spawning may change, often quite dramatically (Flagg *et al.*, 1995; Ford *et al.*, 2006; Quinn *et al.*, 2002). Such differences in spawning date are likely to have large fitness consequences, as this trait is closely linked to the prevailing regimes of temperature, flow and productivity of the ecosystem.

The *genetic* outcomes of domestication selection and their potential solutions have rarely been tested empirically in salmonids due, in part, to the fact that such experiments require a breeding design and these species are long lived. Even in those populations in which domestication selection has been reported in controlled experiments, few studies have been designed to detect this phenomenon directly. An experiment conducted over several generations (Hershberger *et al.*, 1990) implicated domestication selection for increased weight in coho salmon cultured over four generations in marine net pens. However, the underlying genetic model in this study has been criticized (Hard, 1995) because the experiment did not maintain controls that may have discriminated environmental versus genetic changes during culture.

In a seminal study, wild steelhead embryos released in small streams generally had a higher survival to 1 year than those of either hatchery or hybrid offspring (Reisenbichler and McIntyre, 1977). In this case, hatchery fish were derived from the wild population and separated for only two generations. Results differed between streams, suggesting a genotype by environment interaction that was magnified in some environments but not others (Hard, 1995). Hence, the severity of domestication selection can be expected to vary in wild environments. As a comparison, in a recent experiment mimicking the experimental design of Reisenbichler and McIntyre (1977), differences in growth and survival were not seen between the offspring of wild brown trout, a sea-ranched strain and their hybrids when they were reared in the wild (Dahl *et al.*, 2006; Dannewitz *et al.*, 2003). The sea-ranched strain had been separated from its source population by seven generations. These contrasting examples highlight the importance of experimental design—the sea trout experiments were conducted in a common environment, were replicated and took into account genetic effects that may explain variation between individual families comprising each cross type.

It is quite clear that the risks posed by domestication selection have not been quantified in a *systematic* fashion. In articles examining genetic changes in hatchery salmon populations, many authors have recognized domestication selection as a potentially significant problem (Busack and Currens, 1995; Waples, 1999), but have concluded that scant evidence exists to evaluate its significance to management approaches. Little is known about the relationship between selection on specific fitness traits and population size, the number of generations in captivity that may lead to genetic differences with the wild population and whether such selection is reversible or avoidable through different management approaches. Such knowledge is essential for conservation planning, and there is an urgent need for research on the extent and consequences of domestication selection in salmonids, as well as steps that may be taken to reduce its effects.

5.1.1.2. Hatchery regime effects on wild fish If the hatchery regime results in a change in the genetic composition of the captive population, then such changes can have negative consequences on the wild populations with which they interact. These changes can be demographic in nature; the release of a genetically under-represented hatchery population into the wild can reduce the overall effective population size N_e of the two components together or decrease the existing population structure. The changes can also affect the fitness traits of a wild population through hybridization with less fit hatchery fish. Taken together, the results of these processes can lead ultimately to the decline and extinction of an endangered wild population.

5.1.1.2.1. Changes in effective population size A simple simulation based on the Ryman–Laikre model (Ryman and Laikre, 1991) can be used to illustrate the effects of hatchery release size on a population's effective size, N_e (Hedgecock and Coykendall, 2007). The model examines the effect of hatchery recruitment to a wild population over a *single* generation, and relies on known values of effective size for hatchery (N_{eh}) and wild (N_{ew}) fish. Outcomes vary with the relative proportion of hatchery fish in the total census population (Fig. 2.19). Intuitively, supplementation with a hatchery population with a large N_e is beneficial when the wild population has a small N_e (Fig. 2.19A), but detrimental with the opposite scenario (Fig. 2.19C). The most interesting lesson to be learned from this model, however, is that the effects of hatchery supplementation can be very detrimental to wild populations of moderate effective size (Fig. 2.19B).

One needs to keep in mind that N_e is less than N in most cases. For example, the Ryman–Laikre method assumes that all fish are spawning adults, but many hatcheries release smolts with different return rates than the wild fish. Similarly, it is assumed that hatchery and wild fish have an

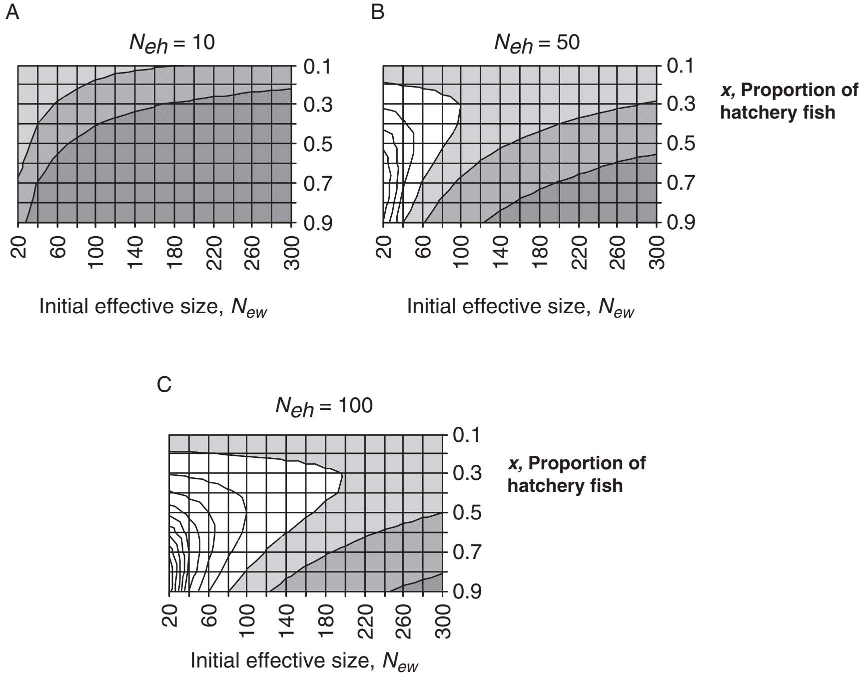

Figure 2.19 Proportional change in the effective population size of a supplemented population (N_{es}), following a single release of a hatchery population of varying effective sizes (N_{eh}). Shaded areas represent decreases in the effective size of the supplemented population. Each contour line represents a proportional increase or decrease by a factor of 2. Based on approaches developed by Ryman and Laikre (1991) and Hedgecock and Coykendall (2007) where $N_{es} = (N_{eh}N_{ew})/(x^2N_{ew} + y^2N_{eh})$, and N_{ew} is the effective size of the wild population prior to supplementation, x is the relative proportion of hatchery-origin fish, y of wild fish, and $x + y = 1.0$.

equal chance of reproducing successfully, but many studies have shown that this is not the case. The approach also assumes that the numbers of progeny from captive or wild fish are distributed binomially, and that there are no overlapping generations. This model has been further developed, taking many of these caveats into account, and the newer models will be discussed in a later section. The central point to be made from this model, however, is that attempts to increase the growth rate of a population may be detrimental to the genetic diversity of a population if few individuals are used to recover that population (Ryman and Laikre, 1991).

5.1.1.2.2. Hybridization and outbreeding depression The impacts of hatchery releases may be limited to a change in effective population size if the hatchery stock is genetically identical to the wild population with which it interacts. However, if genetic variation in hatchery stocks changes following inbreeding or domestication selection, or if hatchery fish are exogenous to the wild system, then hybridization between the cultivated fish and the wild fish may have unintended consequences. Hybridization between unrelated populations can lead to a reduction in fitness, known as outbreeding depression. Outbreeding depression has been attributed to two mechanisms, each of which can have different long-term consequences.

First, outbreeding depression can result from a loss of local adaptation (known as ecological outbreeding depression). Populations can become adapted to a specific environment following selection. Such 'local adaptation' is extensive in the salmonids (Allendorf and Waples, 1996; Taylor, 1991; Waples *et al.*, 2001), and there is substantial concern that hybridization will result in its loss (Allendorf and Waples, 1996; Busack and Currens, 1995). If individuals from unrelated populations mate, hybrids have only half the 'adapted' alleles in either parental environment and are not as fit as the parental populations. This reduction in fitness is often seen in the first (F1) hybrid generation. Second, outbreeding depression may follow a disruption of interactions between co-adapted genetic loci underlying fitness traits (known as physiological outbreeding depression). These epistatic interactions can arise either through selection, which can act concurrently on genes that are inherited together, or through chance associations (Lynch and Walsh, 1998; Templeton, 1986). Significantly, co-adapted gene complexes can differ between populations occupying similar environments, and recombination between divergent genomes can disrupt such complexes. Typically, hybrid vigour (heterosis) observed in the F1 hybrids is a poor indicator of the performance of subsequent generations (Lynch and Walsh, 1998) because recombination between the parental chromosomes occurs for the first time in this generation.

It has been hypothesized that the underlying mechanisms for outbreeding depression will have different outcomes for hybrid populations. Simulations have shown that a disturbance of local adaptation results in a greater initial fitness decline than a disruption of co-adapted gene complexes (Edmands and Timmerman, 2003). However, the simulation results differ over the long term. Much of the genetic variation explaining local adaptation is additive and provides a better opportunity for population recovery through selection than does the epistatic variation that results from co-adapted gene complexes. Epistatic variation arises through genetic drift and indirect selection (Lynch and Walsh, 1998).

The severity of outbreeding depression is expected to change with a number of parameters and there is a considerable body of literature investigating whether such parameters can be used to predict the outcomes of hybridization. For example, the incidence of outbreeding depression is expected to increase with greater genetic distance between hybridizing taxa (Emlen, 1991; Lynch, 1991). This prediction is true across a wide range of species, but not in others (Edmands, 2002). Declines in fitness may depend on prevailing environmental conditions (Lynch, 1991). These environments may fluctuate temporally and results may vary accordingly (Gharrett *et al*., 1999; Gilk *et al*., 2004). Most studies investigating the consequences of hybridization are on first generation hybrids only, but outbreeding depression can be expected to vary across generations (Edmands and Timmerman, 2003). Thus, fitness increases in first-generation hybrids are not necessarily repeated in the second generation (Fenster and Galloway, 2000), and population recovery can vary (Edmands and Timmerman, 2003; Templeton, 1986). Finally, the expression of outbreeding depression differs across fitness traits (Andersen *et al*., 2002).

A meta-analysis on several studies in fishes has shown that the outcomes of hybridization are difficult to predict (McClelland and Naish, 2007). Response varies across traits, taxon and generation but, significantly, genetic distance based on neutral genetic markers cannot be used reliably as an indicator of the incidence of outbreeding depression. Such an outcome can be explained by the unpredictable nature of the different mechanisms underlying outbreeding depression (Lynch and Walsh, 1998), but also by the fact that a measure of genetic distance at fitness traits may be more appropriate for this task (McClelland and Naish, 2007). In a recent review, Utter (2001) proposed that the *complexity* of life history might be a better predictor of outbreeding depression because introgression is more likely in freshwater than in anadromous salmonids, and hybrids of the latter may be less likely to survive.

In salmonid fishes, both increases and decreases in fitness have been observed in the F1 generation. Decreases have been observed in pink salmon homing ability (Bams, 1976), disease resistance in coho salmon (Hemmingsen *et al*., 1986), salinity tolerance in kokanee hybrids (Foote *et al*., 1992), growth rate in coho salmon (McClelland *et al*., 2005; Tymchuck *et al*., 2006) and rainbow trout (Tymchuck and Devlin, 2005) and development rate in coho (Granath *et al*., 2004). However, such decreases were not seen in the F1 of pink salmon (Gharrett and Smoker, 1991; Gharrett *et al.*, 1999).

A few studies have followed outbred populations through to the F2 or subsequent generations (McClelland and Naish, 2007), and individual case studies have shown a continuation in reduced fitness in these generations (McClelland *et al.*, 2005; McGinnity *et al.*, 2003; Tymchuck and Devlin, 2005; Tymchuck *et al.*, 2006). In all of these examples, fitness loss was attributed to genetic mechanisms underlying ecological outbreeding depression. However, it is the systematic treatment of hybridization over varying evolutionary distances that will provide researchers with the ability to predict the genetic outcomes of mixing populations. In a series of experiments on pink salmon populations, researchers in Alaska have performed crosses between populations of varying genetic distance with the intent of detecting the point at which outbreeding depression will no longer be demonstrable. At one extreme, reproductively isolated pink salmon returning strictly in either the odd or the even years were crossed and released. The survival of their F1 hybrids in the wild was comparable to the controls (Gharrett and Smoker, 1991; Gharrett *et al.,* 1999), but the F2 hybrid survival rate was severely depressed (Gharrett *et al.,* 1999). In this case, outbreeding depression was attributed to a breakdown in co-adapted gene complexes, which is perhaps not surprising. The odd and even year pink salmon return to similar habitats and any genetic differences that accumulate between them must be due, in large part, to genetic drift. In contrast, a second experiment has demonstrated that the second mechanism underlying outbreeding depression is loss of local adaptation. Pink salmon from the same year class that were spatially separated by about 1000 km were hybridized and both the F1 and F2 generations exhibited outbreeding depression (Gilk *et al.,* 2004). In contrast to these findings, coho salmon spawning populations separated over spatial distances of 130–340 km and displaying different development rates showed no change in fitness over two generations following hybridization (Smoker *et al.*, 2004), although the authors point out that the power of the data may not have been sufficient to detect outbreeding depression.

These experiments serve to illustrate the potential outcomes of hybridizing unrelated populations, but are most useful when they are systematic in nature. The continuation of experiments such as those conducted on pink salmon over different distances will provide a very interesting insight into whether evolutionary distance can be used as a predictor of the potential for outbreeding depression within a single anadromous salmonid species, a point relevant to effective management.

5.1.1.2.3. Population structure

Increasingly, attention is being paid on the effects of hatchery releases on metapopulation structure of a wild population (Utter, 2004; Ward, 2006). Hatchery activity may affect population structure through two means: by transfers between different locations and by continued release of hatchery fish. For example, Vasemägi *et al.* (2005) demonstrated that ongoing releases of non-indigenous Atlantic salmon resulted in homogenization of population structure of wild fish over time. The impact of the *number* of fish transferred and released on population structure has not been frequently reported, and yet an understanding of this relationship is important for risk assessments. In coho salmon, it has been shown that the number of fish transferred might reduce population structuring, even between closely related populations (Eldridge and Naish, 2007). More importantly, the numbers of fish released from hatchery programmes that collect broodstock locally resulted in a reduction in fine scale population structure in this species (Eldridge and Naish, 2007), a finding that has clear implications for ongoing hatchery programmes. Population structure reflects evolutionary processes, some of which lead to local adaptation, and levels of migration between neighbouring populations are related to the long-term genetic viability of a species as a whole (Waples, 2002). The greater the spatial diversity of a species, the more likely that species will exhibit resilience to extinction risk (McElhany *et al.*, 2000). Ongoing hatchery programmes may need to control the size of their release and numbers of fish transferred between programmes in order to reduce their impact on this resiliency.

5.1.2. Evidence for the genetic impacts of different types of hatchery programmes

In an interesting evaluation of the genetic risks associated with hatchery practises, Campton (1995) raised two key points that are often ignored when evaluating whether hatchery fish can be effectively used as a management tool for conservation or harvest. First, most studies fail to discriminate between the underlying biological or management-based causes of any detrimental effects. In the years between Campton's and this chapter, this distinction has rarely been elucidated. Second, there is a paucity of data providing a clear understanding of the biological causes of such effects. In Section 5.1.2, we examine the evidence for the genetic outcomes of hatchery practises in the context of hatchery type and programme goals, the risks associated with such goals and the evidence, if any, for impacts that may be attributed to biological effects rather than to management effects.

5.1.2.1. Captive broodstock The greatest genetic risks associated with the maintenance of an entirely captive broodstock in culture over long periods of time are the loss of within-population genetic diversity and domestication selection. Losses due to genetic drift may be avoided by maintaining high N_e/N_c ratios and inbreeding can be reduced for as long as possible by maintaining pedigrees and minimizing kinship during mating (Rodriguez-Clark, 1999). In very small populations, selection theoretically becomes almost negligible (unless the selection differential is very high), and some authors have suggested that captive endangered populations be managed as fragmented subpopulations in different rearing facilities in order to avoid domestication selection (Margan *et al.*, 1998). This strategy is risky because significant reductions can be incurred if subpopulations are lost and to date, the approach has been supported empirically in experimental populations of fruit flies only (Woodworth *et al.*, 2002). Perhaps some of the best management steps that can be taken to avoid domestication selection in a captive broodstock are the reduction of the number of generations held in captivity (initiating reintroduction as soon as possible), and decreasing selection differentials between hatchery and wild environments as far as possible.

The scientific community has started to accumulate evidence on the consequences of genetic drift, inbreeding and domestication selection in captive salmon populations, but there are few studies that examine the effectiveness of management steps in mitigating these risks in fishes, let alone salmonids. For example, studies comparing modern to archival samples, such as that conducted on captive Atlantic salmon in the Baltic region (Saisa *et al.*, 2003), demonstrate that long-term programmes have resulted in reduced genetic diversity and effective sizes. However, the extent to which such losses could have been avoided through careful management has not been determined, especially since our awareness of the risks has post-dated the initiation of such programmes. Realistically, the mating of relatives (and hence inbreeding) is inevitable in a closed system despite the best measures (Myers *et al.*, 2001). An inbreeding rate of around 1% is generally deemed acceptable in benign agricultural environments (Franklin, 1980), but this tenet has yet to be tested in salmonids that will eventually be released to the wild.

5.1.2.2. Supplementation through supportive breeding The goal of many conservation-oriented hatcheries is to support declining populations and, thus, most seek to enhance numbers without compromising the genetic diversity of the wild populations. This goal may be difficult to attain because a change associated with broodstock collection and release is probably inevitable (Waples, 1999). Supplementation hatcheries face similar challenges as those described for captive broodstock, but have an advantage in some cases. Many genetic changes such as inbreeding and domestication selection can be theoretically reduced by replenishment from the wild populations, and many recommendations focus on this practise (e.g., Mobrand *et al.*, 2005). However, these programmes may also have a major disadvantage: through their practises, they could alter the genetic composition of the wild stocks with which they interact. This alteration may occur through a change in effective population size, homogenization of locally adapted stocks or through outbreeding depression, and can affect the ability of the vulnerable populations to adapt to a changing environment.

Systematic treatment of the genetic effects of supportive breeding has only occurred through theoretical modelling. Earlier, we described how a single generation of supplementation could result in a decrease in the effective population size of a wild population, even if supplementation leads to an overall increase in the census size (the Ryman–Laikre effect). This first model was important in alerting managers to an important risk associated with supportive breeding, but examined the outcomes of supplementation over a single generation only. Supportive breeding programmes are usually carried out over several generations and are typically considered successful if the programme results in a viable, self-sustaining population.

In a series of modelling exercises, a number of authors have examined the genetic impacts of supplementation under different management and demographic scenarios. The approaches used can be divided into two groups: one focused on effective size or inbreeding and the related effects on drift (Duchesne and Bernatchez, 2002; Wang and Ryman, 2001; Waples and Do, 1994), and the other on measures related to fitness differences between the two components of the population (Ford, 2002; Lynch and O'Hely, 2001; Theodorou and Couvet, 2004). All models were based on several necessary assumptions and attempted to identify the conditions under which supplementation programmes are detrimental or beneficial to vulnerable wild populations. Both groups have implicit links to the other, but an integrated model that addresses the effects of both drift and domestication (or relaxation of selection) has yet to be developed.

All of the studies demonstrated conditions under which supplementation would be negative. For example, Waples and Do (1994) showed that if a small number of breeders were used in a hatchery, an 'inbreeding crash' would result in the wild population after the cessation of an unsuccessful programme. The relaxation of selection in a hatchery may lead to the accumulation of deleterious mutations through drift (Lynch and O'Hely, 2001), which may in turn compromise any numerical gains in the population. A wild population's mean phenotype can rapidly change towards that of a captive population (Ford, 2002) even when migration between the two is small.

Several management steps such as increasing the N_e of the hatchery population may reduce genetic risks associated with releases, but some theory has shown that this benefit is realized only if the census size of the entire population increases (Wang and Ryman, 2001) or if the contribution of captive populations is moderated (Theodorou and Couvet, 2004). The rate of inbreeding could be reduced if N_e/N_c ratios were high in the hatchery population (Waples and Do, 1994). Steps such as increasing the migration rate between the hatchery and wild stocks through broodstock replenishment from the wild have the advantage of reducing negative genetic changes (Duchesne and Bernatchez, 2002; Ford, 2002; Wang and Ryman 2001), but the outcomes of using exclusively wild fish for broodstock are complex and depend on the scenarios modelled (Duchesne and Bernatchez, 2002; Wang and Ryman, 2001).

Many models point towards an optimal programme duration. At the initiation of a program, supplementation could be detrimental to the N_e of the wild population because the initial demographic effect of sampling wild individuals to create a broodstock may be negative, and must be compensated for by several generations of support (Duchesne and Bernatchez, 2002; Wang and Ryman, 2001). On the other hand, all the studies caution that supportive breeding programmes may not be genetically beneficial in the long term in many situations. For example, in the selection model of Ford (2002), it was demonstrated that a shift in a wild population's phenotype can still occur within 50 generations in some scenarios modelled, even if hatchery broodstock comprise natural spawners, and that outcomes may depend in part on population growth rate and carrying capacity in the native environment.

Perhaps the strongest message derived from a reading of these six studies is that the outcomes of supplementation are difficult to predict and may be programme-specific [an examination of the scenarios modelled by Duchesne and Bernatchez (2002) supports this view]. Although some broad conclusions could be drawn, each study has caveats even if the model assumptions are correct. Thus, strong emphasis must be placed on monitoring changes in genetic diversity very closely and in developing meaningful performance measures for hatchery programmes.

Little empirical proof supports theoretical predictions of the outcome of management practises, partly because most of this theory is very recent, and many supplementation hatcheries have existed for longer than our awareness of the genetic risks involved. However, several case studies support theoretical predictions; namely, that genetic diversity can be maintained or reduced by hatchery founder numbers (Primmer *et al.*, 1999), sex ratios at mating (Tessier *et al.*, 1997), hatchery population size (Hansen *et al.*, 2000) and effective population size of released hatchery fish (Eldridge and Killebrew, 2007; Hedrick *et al.*, 2000; Tessier *et al.*, 1997). Heggenes *et al.* (2006) reported that measures of neutral genetic variation and population structure did not significantly change after 20 years of supportive breeding, an outcome attributed to the use of overlapping year classes and frequent integration of wild fish into the broodstock. On the other hand, some studies do not fit predictions. In Sweden, a hatchery population of sea trout received no new broodstock from its source wild populations for approximately seven generations (Palm *et al.*, 2003), but was used to supplement the wild populations, thereby creating unidirectional gene flow. Effective population size was high in the captive population and, while small genetic differences were seen between both captive and wild fish on a yearly basis, these differences were outweighed by temporal variation (Palm *et al.*, 2003). The hatchery stock used in this study was the same population that showed little sign of domestication selection described earlier (Dannewitz *et al.*, 2003).

Studies on stray rates from supplementation hatcheries are rare and the extents to which fish from such programmes interbreed with wild fish are unknown. There are several examples of close genetic relationships between locally derived hatchery fish and their wild counterparts (e.g., Hansen *et al.*, 2000; Primmer *et al.*, 1999) and one case in which a wild Chinook population in the Columbia River appears to have maintained its integrity in the face of supplementation in nearby rivers (Marshall *et al.*, 2000). In contrast, Williamson and May (2005) suggested that releases of supplementation hatchery fish in areas that do not correspond to their natal spawning grounds have led to reduced imprinting and widespread straying and homogenization of Chinook populations in California.

A key question relevant to evaluating the potential risks and benefits of supportive breeding is whether hatchery fish are as fit as their wild counterparts and whether they may effectively contribute to conservation efforts (Berejikian and Ford, 2004; ISAB, 2002). Two studies based on measuring the reproductive success of locally derived hatchery fish provide some information on their relative lifetime fitness over the short term. Locally derived coho salmon (Ford *et al.*, 2006) and steelhead (Araki *et al.*, 2007) reared in a hatchery to the smolt stage and released were as successful reproducing in the wild as naturally produced wild fish. These results provide a clear contrast with the reduced reproductive success of exogenous, domesticated Atlantic salmon (aquaculture escapees; McGinnity *et al.*, 1997, 2003) and steelhead (Araki *et al.*, 2007) that have been propagated over several generations. While both studies on the locally derived broodstock provide a somewhat optimistic outlook for conservation programmes, there are caveats attached to both. Ford *et al.* (2006) pointed out that their study was performed on a system which had experienced hatchery releases for over 60 years, and the naturally produced fish were themselves likely propagated in a hatchery in the previous one or two generations. Araki *et al.* (2007) reported that hatchery fish reproducing with each other in the wild produced fewer offspring than expected, which has implications for cumulative fitness losses over several generations of propagation. Both studies emphasize that the long-term effects of supportive breeding programmes are still unknown.

Returning to our stated aim of evaluating whether negative biological effects can be avoided by correct management practises, we conclude that there is insufficient empirical data available, although recent studies on relative fitness of locally derived hatchery fish provide some insight on their possible contribution to conservation efforts, and should be replicated and continued over several generations. The theoretical information has demonstrated that there are scenarios under which correctly managed hatcheries may benefit declining populations, and empirical studies should be carried out within the framework of this theory. However, it is quite clear there are few general statements that are applicable to supportive breeding programmes. Theory has shown that the 'window of opportunity' for rehabilitating populations may be limited to short time periods, and practically, programmes must be accurately monitored to avoid negative effects. The permanent use of conservation-based hatcheries may be risky, since there appear to be substantial genetic risks associated with the failure to sustain large and genetically diverse populations. The maintenance of such hatcheries therefore depends on risk trade-offs that necessarily relies on clear dialogue between science and policy (Waples and Drake, 2005).

*5.1.2.3. **Production hatcheries in the presence of wild stocks*** The typical production hatchery practise of releasing a closed, and at least partially domesticated, population for harvest opportunity can result in introgression. Introgression may, in turn, lead to a change in the mean phenotype towards that of the hatchery fish, to outbreeding depression and to complete displacement of the wild population.

Although the effects of production hatcheries on wild fish have not been explicitly modelled, many of the theoretical treatments examined above provide insight on the outcomes of such programmes. If a closed, captive population makes a large contribution to the breeding pool, genetic load may increase substantially over the long term (Lynch and O'Hely, 2001; Theodorou and Couvet, 2004), but even low levels of gene flow from the hatchery to the wild populations can move the optimal wild phenotype towards that of the hatchery fish (Ford, 2002). None of the theoretical studies explicitly model the use of exogenous and domesticated stocks that have been typically used in production hatcheries. Some recent empirical evidence for the outcomes of releasing hatchery fish are summarized in Table 2.2, but few general trends can be inferred from the systems studied because release numbers, duration of releases and broodstock management have been poorly documented. Hatchery releases pre-date any concerted scientific studies and in many cases in Europe stocking has been practised for 150 years or more (Berrebi *et al.*, 2000a; Laikre, 1999).

There is extensive evidence that hatchery-wild hybrids from production hatcheries are less fit than wild fish (Table 2.2) and rates of introgression vary with life history strategies. For example, studies in brown trout indicate that introgression rates are higher in resident than anadromous forms. The more complex life history of the anadromous forms probably precludes completion of the life cycle (Ruzzante *et al.*, 2004). In a review paper, Utter (2001) noted that anadromous fish from different evolutionary lineages are less likely to hybridize with each other than those within lineages. In support of this view, Ford *et al.* (2004) reported that introduced coho populations from Washington State did not appear to persist in Oregon, whereas transfers between closely related populations appear to have affected population

Table 2.2 Summary of genetic effects of hatchery fish on wild fish, categorized by source of hatchery fish and species

Species and life history	Region	Outcome	Study
Exogenous source of hatchery fish			
S. trutta, anadromous	Denmark	Reduction in fine-scale population structure, level of introgression correlated with intensity of release activity	Fritzner *et al.*, 2001; Ruzzante *et al.*, 2001
		Low incidence of released fish. Hatchery fish provided little harvest opportunity for the anadromous population, but introgressed with the resident forms	Hansen, 2002; Hansen *et al.*, 2002
		Decline in incidence of domesticated fish following cessation of releases	Fritzner *et al.*, 2001; Ruzzante *et al.*, 2004
	Norway	Mortality of hatchery fish at early life history stages was higher than wild fish, may reduce incidence of introgression	Borgstrom *et al.*, 2002
S. trutta, resident	Norway	Hatchery fish hybridized with wild fish, but survival of hybrids was lower than wild	Skaala *et al.*, 1996
		Little impact of hatchery on wild fish population structure, despite 40 years of stocking	Heggenes *et al.*, 2002
	Spain	Extensive introgression in all populations studied, reduction of population structure	Cagigas *et al.*, 1999; Garcia-Marin *et al.*, 1998; Machordom *et al.*, 1999, 2000

(*continued*)

Table 2.2 (*continued*)

Species and life history	Region	Outcome	Study
		Release of hatchery fish did not improve population size	Machordom *et al.*, 1999
		Straying of hatchery fish from areas that received releases versus ones that did not. Hatchery genotypes persisted after cessation of releases	Cagigas *et al.*, 1999
		Lower incidence of introgression in harvested regions than in protected areas	Garcia-Marin *et al.*, 1998, 1999
		Decline in alleles of domesticated origin 7 years after cessation of releases	Almodovar *et al.*, 2001
	France	Some selection against hatchery fish, but cessation of releases for 6 years did not lead to recovery of wild genotypes	Poteaux *et al.*, 1998a,b
		Levels of introgression varied with intensity of release activity	Aurelle *et al.*, 1999; Poteaux *et al.*, 2000
		Incidence of introgression was small annually, but accumulation of hybrid genotypes increased over time. Incorporation of locally derived broodstock may have maintained population variation	Berrebi *et al.*, 2000a

	Switzerland	Introduction of domesticated strain reduced reproductive barriers between two indigenous forms	Largiader and Scholl, 1995
		Degree of admixture was site specific and may be linked to management actions—intensity of release activity and fishing	Largiader and Scholl, 1996; Mezzera and Largiader, 2001a; Mezzera and Largiader, 2001b
		Hybrids between hatchery and wild fish were less fit than wild fish, mortality of hybrids greater between age 1+ and 2+. Hybrids were more vulnerable to fishing	Mezzera and Largiader, 2001a,b
	Italy	Reduction in genetic diversity and structure, replacement of wild subspecies with hatchery fish	Marzano *et al.*, 2003
S. salar, anadromous	North America, east coast	Evidence that past release activities reduced stock structure in some drainage systems	King *et al.*, 2001
	Denmark	Translocations or hatchery releases have had little effect on long-term population structure	Nielsen *et al.*, 1999
	Estonia	Release of hatchery fish compromised recolonization of restored habitat by indigenous populations	Vasemägi *et al.*, 2001
O. mykiss, anadromous	United States, west coast	Increased straying by non-native hatchery fish	Schroeder *et al.*, 2001

(*continued*)

Table 2.2 (*continued*)

Species and life history	Region	Outcome	Study
		Hatchery females had lower reproductive success than wild fish	Kostow *et al.*, 2003
		Introduced summer run hatchery fish hybridized with indigenous winter run populations	Mackey *et al.*, 2001; Kostow *et al.*, 2003
		Hatchery fish were more abundant on spawning grounds and produced more offspring, despite lower reproductive success	Kostow *et al.*, 2003
O. mykiss, resident	United States, west coast	Introgression led to a reduction in disease resistance in indigenous population	Currens *et al.*, 1997
O. clarkii, resident	United States, west coast	Rainbow trout/cutthroat trout hybrids were difficult to detect in generations later than the F1 in the wild, provided a mechanism for undetected introgression	Campbell *et al.*, 2002
O. tshawytscha, anadromous	United States, west coast	Population structure persisted, despite extensive hatchery releases	Utter *et al.*, 1995
Salvelinus umbla, resident	European Alps	Extent of introgression was small and varied across environments	Brunner *et al.*, 1998
		Higher introgression of hatchery fish in a lake disturbed by pollution than one that remained undisturbed	Englbrecht *et al.*, 2002
Salvelinus nyamacush, resident	United States, southeast	Extent of introgression with non-native northern form varied from replacement to	

		no detectable hybridization. Erosion of population structure, level of introgression not related to intensity of release activity	Galbreath *et al.*, 2001; Hayes *et al.*, 1996;
Endogenous source of hatchery fish			
S. trutta, anaromous	Poland	Reduction in genetic diversity within hatchery stocks	Was and Wenne, 2003
S. salar, anadromous	Ireland	No differences in survivorship observed between hatchery and wild fry at 18 months	Crozier and Moffett, 1995
		Locally derived hatchery fish exhibited similar return numbers but different life history. Translocated population from neighbouring drainage had lower return rates	McGinnity *et al.*, 2004
O. tshawytscha, anadromous	New Zealand	Significant changes observed in male life history characters and in return timing. Population was introduced from California	Unwin and Glova, 1997
O. gorbuschi, anadromous	Alaska	Hatchery derived from local broodstock appeared to have no affect on wild population structure in the same locality	Seeb *et al.*, 1999

structure in the same species (Eldridge and Naish, 2007). The incidence of hybridization within freshwater salmonids appears to vary greatly (Table 2.2). Hybridization between hatchery and wild fish can be extensive and detrimental (Cagigas *et al.*, 1999; Garcia-Marin *et al.*, 1998), with little benefit to the population size (Machordom *et al.*, 1999). On the other hand, descendants of hatchery fish may be undetectable even after a long period of hatchery releases (Heggenes *et al.*, 2002). Many studies report greater introgression with higher release numbers (Aurelle *et al.*, 1999; Mezzera and Largiader, 2001a), but others did not (Hayes *et al.*, 1996). Some authors observed a decline in hybrid genotypes after releases are stopped (Almodovar *et al.*, 2001), but these genotypes persisted in other areas (Poteaux *et al.*, 1998a). There is also some evidence that the incidence of hybridization may be environmentally or ecologically dependent. Arctic charr (*Salvelinus umbla*) released into an undisturbed lake in the Alps were less successful at becoming established than those released into a historically polluted one (Englbrecht *et al.*, 2002).

Management strategies for production hatcheries have been proposed in order to avoid the negative impacts of hatchery fish on wild populations (ISAB, 2002; Mobrand *et al.,* 2005; Utter, 2004). Utter (2004) has suggested that the domestication of hatchery broodstock can be expected to lead to substantially reduced fitness of hatchery fish in the wild. The release of such stocks may be beneficial under management scenarios that are aimed at deliberately segregating hatchery and wild fish, because reduced fitness of hatchery fish would minimize concerns about the impacts of colonization and hybridization. There is not yet sufficient data to determine whether this is a viable strategy; while many studies report hybridization between less-adapted hatchery and wild fish (Table 2.2), there have been few concerted efforts at deliberately domesticating 'maladapted' hatchery fish for segregated programmes and tracing their reproductive success in the wild. There are some existing approaches that may support this goal, however. For example, certain steelhead production hatcheries in the United States have introduced non-native populations that differ in their run timing and spawn timing from indigenous populations. While the effects of these programmes have not yet been fully characterized, it appears that the life histories of the hatchery fish may change in response to the new environment and in some examples, return timing and spatial distribution have been seen to overlap with that of the wild fish (Mackey *et al.*, 2001), making introgression with wild individuals possible, but in one case, limited (Kostow, 2004). Cutthroat trout (*O. clarki*) are deliberately hybridized with rainbow trout (*O. mykiss*) because the hybrids can be identified from the parental species phenotypically and can be targeted by anglers. However, hybrid individuals of generations later than the F1 cannot be reliably identified and hence escape capture, leading to ongoing inter-specific introgression (Campbell *et al.*, 2002). Segregation can be controlled, to some extent, by complete harvest of the hatchery population. Brown trout hatchery fish in one study appear to be more susceptible to angling (Poteaux *et al.*, 1998a), and a review of programmes in Spain showed that there are lower levels of introgression in harvested than protected regions (Garcia-Marin *et al.*, 1998). However, such an approach relies on efficiency of capture.

Given these caveats, Mobrand *et al.* (2005) have recommended that an alternative strategy could be considered, the integration of hatchery fish and wild fish. Fish surplus to the maintenance of the wild population may be harvested. The use of endogenous sources of broodstock for production hatcheries has both positive and negative aspects. Using native stocks may reduce losses associated with the production of less fit hybrid individuals typical of exogenous fish releases. For example, a pink salmon hatchery using locally derived broodstock appeared to have had little effect on the population structure of indigenous wild populations (Seeb *et al.*, 1999). A second hatchery collects broodstock migrating into PWS destined for different regions, and the hatchery fish released comprised a mixture of stocks with greater potential to affect local populations. On the other hand, it may also be argued that exogenous fish are more likely to be purged from a wild population, especially if a programme is terminated. There is also some evidence for change in life histories, even when endogenous fish have been used and fish have been reared for part of their life cycle in the hatchery (McGinnity *et al.*, 2004) sometimes causing a subsequent shift in such traits in the wild population (Unwin and Glova, 1997). Finally, theoretical approaches have shown that long-term integration between hatchery and wild stocks is not always a sustainable strategy, which is further exacerbated if that stock is subject to harvest (Goodman, 2005). These studies emphasize the need for further research on the impact of broodstock management and release.

In summary, published studies show that production hatcheries have been detrimental to local wild populations where the two populations interact, although there are many examples where distantly related populations do not appear to have persisted. It should be noted that many genetic studies have focused primarily on reporting levels of introgression only, and results are rarely correlated with the size of release. It is also possible that less fit hybrid individuals may have reduced the overall effective population size and structure of wild fish, thus causing changes in the life history of wild populations, and this aspect should also be studied in greater depth. It is still difficult to ascribe outcomes of production hatcheries to management or biological causes. Management strategies for production hatcheries advanced thus far would be to maintain the hatchery and wild fish as separate populations (Mobrand *et al.*, 2005; Utter, 2004), or to integrate hatchery and wild populations (Mobrand *et al.*, 2005), but the efficacy of these approaches over the long term has yet to be demonstrated empirically.

5.1.2.4. Introduced species The greatest genetic risk associated with the introduction of a new salmon species to a habitat is hybridization with native indigenous populations. Hybridization in this case has three primary genetic outcomes: introgression, repeated introgression leading to hybrid swarms in which neither of the parental genotypes persist, or sterility and hence lost reproductive potential (Allendorf *et al.*, 2001; Leary *et al.*, 1995).

Hybrids of brown trout and Atlantic salmon tend to be unidirectional and may compromise one species through introgression, but not the other (Garcia-Vazquez *et al.*, 2004; McGowan and Davidson, 1992). Hatchery releases have led to hybridization between these two species (Jansson and Oest, 1997), and although outside the realm of this chapter, has increased following escapes from salmon farms in Europe (Matthews *et al.*, 2000). The widespread introduction of rainbow trout for angling has threatened the genetic integrity of many western freshwater species in North America (Leary *et al.*, 1995; Scribner *et al.*, 2000). For example, rainbow trout form fertile hybrids with cutthroat trout (Allendorf and Leary, 1988) and introgression can be greater in regions of hatchery introduction than in areas where the two species co-occur naturally (Docker *et al.*, 2003). Many populations have been replaced by hybrid swarms (Allendorf and Leary, 1988; Williams *et al.*, 1996), which are of no evolutionary or conservation value (Allendorf *et al.,* 2001). Similar results have been recorded in Europe, for example, in areas where brown trout have been introduced to marble trout (*S. marmoratus*) habitats (Berrebi *et al.*, 2000b). Interactions between native bull trout (*Salvelinus confluentus*) and introduced brook trout (*Salvelinus fontinalis*) result in unidirectional hybridization (Kanda *et al.*, 2002), and reproductive effort is substantially compromised in the former species because bull trout tend to be the maternal contributor. The majority of fish are F1 hybrids, with very few backcrosses detected (Kanda *et al.,* 2002). Therefore, bull trout populations are demographically compromised by the reduced reproductive output following the introduction of brook trout for fishing purposes. Finally, the introduction of a new species for harvest opportunity may also have indirect genetic effects on native populations through competition and restriction of the ranges of native populations.

5.1.3. Can management practises negate genetic impacts?

To summarize this section of the chapter, we evaluate whether the current state of knowledge provides guidance on management steps that may be taken to reduce the genetic risks associated with different salmon hatchery programmes. In the decade since Campton (1995) noted that distinction between management and biological risks were rarely elucidated, the majority of research has shown that hatcheries can affect genetic diversity within hatchery populations, and that interactions between hatchery and wild populations can be detrimental. However, a growing number of studies have shown that specific steps in broodstock management have led to both negative and positive outcomes. In recent years, a shift in the research is beginning to move from reporting problems associated with individual case studies towards researching possible solutions, driven in part, by attempts to reform hatchery practises. A key need in this area, therefore, is the development of a strong understanding of the *degree* to which specific activities pose a risk and whether proposed management approaches are effective at reducing these risks.

If we consider the diverse biological outcomes of hatchery rearing, there are still a significant number of unanswered questions. Accumulating evidence has shown that inbreeding in salmonids leads to fitness declines, and these declines vary by the trait measured. However, the relationship between inbreeding and the point at which inbreeding depression becomes manifest is still unclear. In other words, at what population sizes and generation can we expect a decline in fitness due to inbreeding? The answer is unlikely to be simple and can be extended to exploring how the incidence of inbreeding depression is related to historical inbreeding levels, to different wild environments, to life history strategy and to rate of inbreeding. The related management questions would therefore be concerned with developing strategies to both avoid and recover a population from suffering inbreeding depression.

Domestication selection remains a controversial topic, and research thus far has been directed at describing individual case studies that provide evidence of this phenomenon. Measuring the *magnitude* and *direction* of domestication selection under different selection regimes typical of hatcheries, and testing whether the genetic outcomes are reversible if selection is relaxed, is necessary. Research relevant to management should be directed towards evaluating strategies to reduce the magnitude of domestication selection by integrating wild individuals into the broodstock, as well as understanding the relationship between selection and population size and generation number in order to gain an understanding of the duration over which hatchery programmes should be maintained.

Theoretical treatments of the demographic and fitness effects of hatchery releases on the genetic variation and effective population size of wild populations have proved very informative and have illustrated the potential of various management approaches. It is important to provide empirical support of steps aimed at maximizing effective size and reducing demographic effects of releases on the wild populations. Systematic approaches are ambitious and long-term, but can be accommodated by close monitoring of a large range of existing hatchery programmes.

Fitness declines associated with outbreeding have been clearly demonstrated in a large number of studies. However, if a threatened population requires rehabilitation by the introduction of new broodstock, it is still unclear how closely related donor and recipient populations should be in order to avoid outbreeding depression. It appears that genetic distance may prove an unreliable measure, but few studies have examined the relationship between measures of a range of evolutionary distances and the probability of outbreeding depression within a given salmonid species. Management-related research should be directed towards determining acceptable levels of introgression and understanding how evolutionary distances relate to these levels.

Many of these questions are difficult to answer, particularly because they require prolonged experimental periods and substantial support. We emphasize that hatchery-directed research has thus far focused on reporting the genetic outcomes of specific programmes, with only recent exploration of the relationship between these results and management actions. In our chapter [and that of Campton (1995)], we have found little evidence of this delineation and, unfortunately, little insight into whether research programmes are now being directed towards exploring this relationship. This weakness has been exploited by opposing viewpoints on whether hatchery fish should be permitted to spawn in the wild (Brannon *et al.*, 2004a; ISAB, 2002).

If we accept the likely outcome that hatchery programmes will persist, then two general research directions should be implemented in order to provide practical management advice. The first should focus on developing a clear understanding of the relationship between genetic risks involved in hatchery releases, and steps to reduce these risks, even if these experiments are expected to take place over several generations. Most hatcheries have been established without research programmes, and a strong emphasis should be placed on devoting at least a portion of the rearing space to experimental releases. It is only by directly comparing a network of experiments in hatcheries with similar goals that many of the risks and management approaches may be quantified. The second direction should focus on developing a risk averse approach to management, as advocated by Waples (1991, 1999), which implements strict monitoring protocols. These protocols should track fitness changes in hatchery and wild populations using a mixture of approaches. Such data could also contribute significantly to a large meta-analysis that would allow evaluation of the genetic risks posed by releasing cultured fish into the wild. Hatchery programmes have existed for many decades, yet surprisingly, a large programmatic approach to answering many outstanding questions about genetic risks and remedial management practises has yet to be executed. We strongly advocate such research.

Finally, it is important at this point to raise the social context in which research in this discipline is conducted. Waples (1999) and Waples and Drake (2005) pointed out that genetic changes associated with hatcheries are inevitable. Research will likely determine the genetic consequences of hatchery programmes, but societal values must be consulted to determine the degree to which these consequences are acceptable. Efforts to improve the interaction between the two are strongly encouraged.

5.2. Behavioural and ecological interactions between wild and hatchery-produced salmon

There are important implicit (though seldom explicit) assumptions of hatchery programmes regarding ecological and behavioural processes. Violation of these assumptions may result in lower than anticipated production either from the hatchery or from the region that includes hatchery and coexisting wild populations. First, it is assumed that the hatchery increases the abundance or survival of salmon populations during the life history stage that limits the wild population size and that subsequent stages are not limiting. Second, it is assumed that there are no significant interactions between wild and hatchery fish that would limit the enhancement effort. This section briefly reviews these issues, with emphasis on competition between wild and hatchery fish, and a brief consideration of predation.

5.2.1. Competition between wild and hatchery fish

The majority of lifetime mortality in salmonids generally takes place during the period from fertilization to emergence from the gravel several months later. Much of this mortality results from poor circulation of water or low dissolved oxygen concentration (often related to fine sediment), scour from flooding, desiccation or freezing and disturbance by the digging of other female salmon (Quinn, 2005). It has been known for well over a century that salmonid eggs and milt can be taken from adults, mixed and the embryos incubated with higher survival rates than commonly occur in nature [reviewed by Bottom (1997) and Lichatowich (1999); see also Section 2]. Early hatchery programmes were predicated on the assumption that increased number of fry released into the rivers would produce commensurate increases in adults. However, the extent to which this is true depends on the species involved. Almost all salmonid species characteristically emerge from stream gravels and rear for months or years in the stream before migrating to the sea, a lake or a larger river. The generally low productivity of streams caused these species (e.g., coho and Chinook salmon, rainbow and cutthroat trout, Atlantic salmon, brown trout, Arctic charr) to evolve territorial behaviour. Juveniles defend territories from conspecifics and heterospecifics with stereotyped displays and overt aggression. Decades of research have indicated that food and space limit the density of juveniles and production of smolts from streams (Bradford *et al.*, 1997; Chapman, 1966), though habitat quality (e.g., Sharma and Hilborn, 2001) and environmental conditions cause production to vary among sites and years.

The ability of individuals to acquire and retain high-quality feeding territories depends on a number of interrelated factors. Not surprisingly, larger fish dominate smaller ones, and even a small size disparity is sufficient to determine the outcome of a contest, but territorial possession also strongly influences competition (e.g., Abbott *et al.*, 1985; Huntingford and Garcia de Leaniz, 1997; Rhodes and Quinn, 1998). Both of these factors favour early emerging fry because they will hold territories and will have grown by the time that later emerging fry try to compete with them (Einum and Fleming, 2000), though predation may serve as a countervailing pressure (Brännäs, 1995). There are many other factors affecting dominance relationships, including recent experience in territorial bouts, individual recognition, sibling recognition and metabolic rate. However, individuals that are unable to obtain territories may adopt non-territorial 'floater' behaviour patterns (Nielsen, 1992) or be forced to emigrate (Chapman, 1962).

Given the limited food and space in streams, salmonids evolved under high levels of competition among juveniles. Even under some fishing pressure, far more juveniles emerge from the gravel than can be supported in the stream. Thus, for these species it is the fry to smolt period rather than the egg to fry period that is really the limiting life history stage, assuming an adequate number of adults return to spawn. Therefore, the release of hatchery-produced fry or parr into a stream may not increase the number of seawards migrating smolts due to simple competition. However, the hatchery fish may differ from the wild fish in phenotypic traits affecting dominance. For example, if they are fed for some period in the hatchery prior to release then they may be larger than the wild fish. In addition, the timing of spawning in many hatchery populations diverges, commonly becoming earlier than the wild population from which it was derived (e.g., Flagg *et al.*, 1995; Quinn *et al.*, 2002). This difference would magnify any disparity in size between wild and hatchery fish. Nickelson *et al.* (1986) studied 30 streams, half of which had received presmolt coho salmon from hatcheries, and half were unaffected by such activity. Hatchery releases increased the overall density of coho salmon but decreased the abundance of wild coho. Similar numbers of adult salmon returned to the two types of streams but the hatchery-origin fish tended to return earlier in the season and produced fewer offspring, so the hatchery releases failed to increase the productivity of the recipient streams. The authors of this finding suggested that competitive displacement may have been a mechanism underlying this outcome, but this mechanism was not explicitly tested in their study.

There have been many comparisons between the behaviour of wild and hatchery fish in laboratory experiments and also many field studies of the effects of adding hatchery fish to a population of wild or naturally rearing fish, for example, brown trout (Berg and Jorgensen, 1991; Jorgensen and Berg, 1991) and coho salmon (Rhodes and Quinn, 1999). The latter type of study is relevant but, as Weber and Fausch (2003) pointed out, very few have distinguished the effects of competition per se from the effects of increased density. In most cases, growth or some other performance measure was recorded in a population of wild fish, and compared to that in a group of wild fish to which hatchery-produced fish were added. In such cases a ‘substitutive’ experimental design that controlled for overall fish density might be more informative about the processes of competition, though perhaps less representative of the normal management practise.

Competition for food and space in streams may limit many salmonid species, but this is not the case for pink, chum and sockeye salmon. These species commonly spawn at much higher densities than the other species of Pacific salmon and are much more numerous overall. Pink and chum salmon migrate directly to sea after emergence and make little or no use of streams for rearing, whereas sockeye salmon typically migrate to lakes. Conventional wisdom had maintained that salmonids were limited by freshwater constraints but that the ocean had the capacity to rear more salmonids than the rivers could produce. Thus, increases in production of juvenile pink and chum salmon should be accompanied by proportional increases in adults; sockeye salmon might be limited by either spawning or lacustrine rearing capacity. However, between the streams and the ocean lies the estuary, a habitat whose role in salmonid ecology is not fully understood (Thorpe, 1994). Is the estuary a critical habitat, merely a highway through which they must migrate or possibly a hazardous place filled with predators? Generally speaking, the species that enter the estuary at a large size move through it more rapidly than smaller salmonids. Atlantic salmon and sea trout are large when they migrate to sea, as are steelhead, cutthroat, sockeye, coho and yearling Chinook salmon. Chum salmon smolts are small, as are populations of Chinook salmon that migrate to sea in their first year of life, and these species make the most extensive use of estuaries (Healey, 1982a; Simenstad *et al.*, 1982). Pink salmon are something of a paradox as they are the smallest in size on entry into the ocean but seem to move through estuaries faster than chum salmon. Size of smolts and growth in the estuary provide an advantage in survival at sea (Healey, 1982b; Neilson and Geen, 1986; Reimers, 1971). Though growth rates in estuaries are often rapid, the vast majority of juvenile salmonids leave after a few days or weeks, and there is evidence for food limitation in estuaries (Reimers, 1971; Sibert, 1979; Wissmar and Simenstad, 1988). However, the extent to which estuaries present a bottleneck may vary among species. In the Columbia River in the northwestern United States, for example, steelhead, coho, sockeye and yearling Chinook salmon tend to swim in the pelagic zone and remain for only a short time, whereas the under-yearling Chinook salmon are primarily in the littoral zone and are present over a much longer period (Dawley *et al.*, 1986). We know of no systematic, controlled study of the effects of density on wild salmon, or of interactions between wild and hatchery salmon, nor on the duration of estuarine residence and survival of salmon, though such effects might occur.

It is plausible that the estuary is a limiting habitat, given the many millions of smolts that may enter over a short period of time, but can the ocean also be a limiting habitat? Mathews (1980) used data on density, growth and survival of coho salmon in Puget Sound and the Columbia River in the northeastern Pacific to test the hypothesis that increased numbers of hatchery-produced fish depressed the growth or survival of the species, but the data were equivocal. Rogers (1980) noted the strong environmental controls over growth at sea but he concluded that there was a density-dependent reduction in growth of sockeye salmon in Bristol Bay, Alaska, an area where this species is very abundant. Subsequent to that report, a body of evidence developed indicating that the density of salmon at sea affected their growth and age at maturity. Within large 'stock complexes' such as Bristol Bay sockeye salmon and Japanese chum salmon, years with high abundance were usually associated with smaller size (e.g., Kaeriyama, 1998; Rogers and Ruggerone, 1993), though interactions with physical conditions (e.g., temperature) were also noted. For example, the increases in abundance of chum salmon from Hokkaido hatcheries were accompanied by reduced size at age and increased age at maturity (Kaeriyama, 1998). Rogers and Ruggerone (1993) found that the growth of Bristol Bay sockeye salmon was depressed in the final period at sea by their own density but was not affected by other salmon (they were especially interested in possible growth reduction related to the abundance of Japanese chum salmon). However, McKinnell (1995) and Pyper and Peterman (1999) both reported evidence of competition between stock complexes of sockeye salmon.

There is evidence, at least for some of the very large stock complexes, of density-dependent growth. Thus increases in hatchery production might be associated with smaller size and lower survival of those fish, and perhaps for sympatric salmon of the same and even other species (Levin and Williams, 2002), and authors such as Cooney and Brodeur (1998) have discussed the possible implications of marine carrying capacity for salmonid enhancement efforts. However, the extent to which these effects occur in areas with more dispersed production and lower overall densities is unclear. Perhaps more fundamentally, does high density depress only growth or survival as well? Evidence on this crucial point is much less clear, but recently Ruggerone *et al.* (2003) reported that not only the growth but also the survival of Bristol Bay sockeye salmon was depressed by the abundance of Asian pink salmon. In addition, Levin and Schiewe (2001) concluded that under conditions of naturally low ocean productivity, high densities of hatchery Chinook salmon depress survival rates of wild conspecifics. In general, the 1980s and 1990s have seen high abundance and survival rates of Pacific salmon from the northern part of their North American range, and 'predator swamping' effects might lead to a positive relationship between abundance and survival rather than a negative one. Indeed, earlier analysis indicated a positive relationship between survival of Babine Lake sockeye salmon in British Columbia and the abundance of juvenile pink salmon (Peterman, 1982). However, the question certainly needs further work before this finding can be accepted as a general conclusion.

In addition to the potential competition for food and space between wild and hatchery-produced juvenile salmon in streams, and for food in estuaries and the ocean, there are possible competitive effects and behavioural interactions on the spawning grounds. If all wild fish spawned in the river where they originated, and all hatchery fish returned and were spawned in the hatchery where they were produced, these interactions would not occur. However, this kind of segregation seldom occurs. First, there is some straying of hatchery-produced fish into other rivers (Candy and Beacham, 2000; Labelle, 1992; Quinn *et al.*, 1991). Moreover, even if the salmon return to their river of origin, there are often opportunities for exchange between wild and hatchery populations. Nicholas and Downey (1983) reported that the proportion of hatchery-produced Chinook salmon entering Elk River Hatchery, Oregon, averaged 22.8% over a 9-year period (range, 5.9–52.2%). Hence, in most years, the majority of fish produced in the hatchery did not spawn there but rather in the river. In another case of interaction between wild and hatchery salmon, Nicholas and Van Dyke (1982) estimated that 2022 (64.7%) of the 3124 wild coho salmon returning to the Yaquina River watershed in 1981 entered the Oregon Aqua-Foods hatchery. Such decoying of wild salmon into hatcheries both reduces the number of wild fish in the stream and contributes to genetic mixing.

On the other hand, hatchery fish commonly spawn with naturally produced fish and can outnumber them in some systems. In an extreme example, Nicholas and Van Dyke (1982) estimated that 6% of the adult coho salmon returning after release from the Oregon Aqua-Foods, a private production hatchery, strayed to spawn in the Yaquina River watershed, Oregon. However, they were so numerous (and the wild fish so scarce) that hatchery fish constituted 74% of the naturally spawning coho salmon in 1981 (Nicholas and Van Dyke, 1982) and 91% in 1985 (Jacobs, 1988). If a stream's carrying capacity has already been met by the wild salmon, then the addition of hatchery-produced fish will diminish the productivity of the group as a whole, even if there are no functional differences between wild and hatchery fish.

Just as juvenile wild and hatchery salmon differ in phenotype and genotype, with complex implications for their behavioural and ecological interactions, adults differ as well. The nature and extent of the differences vary greatly, depending on whether the wild and hatchery populations have been managed as a single unit (e.g., wild salmon used for spawning in the hatchery and hatchery-produced salmon allowed to spawn naturally, and all salmon subjected to common fisheries) or managed separately. For example, in Washington State, salmon hatcheries have tended to employ the former approach. Until recently, most hatchery-produced salmon were not marked, so fisheries operated equally on wild and hatchery fish, and there was considerable exchange between populations. In such cases the wild and hatchery populations may be essentially the same, and most differences between them may result from culture practises. For example, hatchery smolts are often larger than wild smolts, and this tends to reduce the age at maturity (e.g., Norris *et al.*, 2000), and hence overall size.

On the other hand, steelhead in Washington State have been managed under a very different set of goals. Hatchery steelhead have been selectively bred to return and spawn earlier in the winter than wild fish (e.g., Ayerst, 1977). This approach was initially implemented to lengthen the growing season for juveniles in the hatchery so they could reach a suitable size for smolt transformation and release after 1 year rather than 2 years as is typical of wild steelhead. However, the high genetic variability underlying return date allowed managers to select early returning fish, and hence open early fisheries that targeted the hatchery-produced fish and close the fisheries later if the wild populations needed protection. In this situation, when the hatchery-produced fish spawn in the river, they do so earlier in the year than the wild fish. This approach may expose the hatchery fish to less favourable physical conditions (e.g., flow, temperature or loss of redds to later-arriving wild adults) since presumably the wild fish evolved an optimal spawning season to maximize embryo survival or fry growth. It is therefore perhaps not surprising that the hatchery fish do not produce as many surviving offspring per capita as do wild fish when spawning in the river, as indicated by genetic analyses (e.g., Leider *et al.*, 1990).

5.2.2. Predation

Although most research on behavioural interactions between wild and hatchery-produced salmon has emphasized competition, predation is another important ecological interaction. Salmonids tend to eat invertebrates (e.g., insects in streams and zooplankton in lakes) when they are small but they become more piscivorous once they reach about 10–20 cm (Keeley and Grant, 2001). Studies in freshwater (e.g., Hunter, 1959) and at sea (e.g., Parker, 1971) identified coho salmon as a significant predator on pink and chum salmon. Coho smolts (usually about 10- to 12-cm long) can easily consume newly emerged members of the other species (about 3–4 cm). As the pink and chum salmon grow they become progressively less vulnerable (Hargreaves and LeBrasseur, 1986), but recently Briscoe *et al.* (2005) reported that the survival of Auke Creek coho salmon was positively correlated with the numbers of pink and chum salmon fry released from nearby hatcheries. Likewise, coho salmon in lakes can be a significant predator on sockeye salmon (Ruggerone and Rogers, 1992), and Arctic charr can congregate and eat sockeye salmon smolts (Ruggerone and Rogers, 1984). These latter studies were conducted on wild populations, but releases of large numbers of hatchery-produced coho salmon coincident with the presence or migration of wild salmon could result in significant mortality. Pearsons and Fritts (1999) reported that juvenile coho could eat Chinook that were over 40% of their length (e.g., a 140-mm coho ate a 64-mm Chinook).

There has been a tendency to focus on predation by hatchery-produced smolts on wild fry, but other kinds of predator–prey interactions involving wild and hatchery fish can occur as well. For example, in Lake Washington, Washington State, there is a large population of adfluvial cutthroat trout that prey heavily on wild and hatchery-produced sockeye salmon fry (Nowak *et al.*, 2004). The presence of hatchery fry might buffer predation on the wild fry (as predation is buffered by the abundance of longfin smelt, an alternative forage species for trout), assuming that other factors limit the abundance of trout. However, if the availability of hatchery-produced salmonids increases the abundance or modifies the distribution of predators, increases in predation on wild fish might occur.

5.3. The effects of harvest on wild salmon populations

The underlying principle in the theory of sustainable salmon harvesting is the stock concept. Due to their ability to home to their natal streams, salmon have adapted to a wide range of freshwater habitats, and consist of thousands of reproductively isolated stocks (Helle, 1981; McDonald, 1981). The population dynamics of each stock will be determined by the habitat it uses, and a convenient metric of the overall productivity of each stock is the potential recruits per spawner. A stock that spawns in good gravel with stable flows, little scouring and few fine sediments can be expected to have higher egg to fry survival than a stock spawning in an unstable stream with frequent floods and scour, siltation and intense predation. Similarly, through the rest of the freshwater and marine life history, a stock using better habitat would be expected to have higher survival rates. Higher survival through their life history results in more individuals surviving to return to spawn for every spawner in their parental generation.

On average, a habitat that has less than one recruit per spawner would not be able to support a stock of salmon without frequent immigration. Stocks in good habitat can often produce two to ten recruits per spawner from adults spawning at low density. The sustainable harvest rate for a population depends on the number of recruits per spawner. A population producing two recruits per spawner can be harvested at 50%, one spawner produces two adults, one is harvested and one remains to replace the parental generation and complete the cycle. A population with three recruits per spawner can be harvested at 66%, and a population with four recruits per spawner can be harvested at 75%.

In the absence of harvesting, populations would be expected to increase until competition for resources (breeding space for adults or food and space for their offspring) reduces the recruits per spawner to 1.0; that is, populations cannot grow forever. Thus, when we attempt to estimate the productivity of a salmon population, we normally attempt to estimate the potential recruits per spawner at low densities. Table 2.3 shows the estimated potential maximum recruits per spawner and the exploitation rate at maximum sustainable yield (MSY) for a range of natural populations of Pacific salmon. These estimates were derived from data sets accumulated by R. Myers (Dalhousie University, Canada), and represent only stocks that have been well studied and have survived many generations of harvesting. Therefore, the estimates are almost certainly biased towards the higher end of natural productivity.

Salmon enhancement projects intervene at specific life history stages to improve the survival rates, and thus ideally increase both the recruits per spawner and the potential sustainable harvest rate. For example, if a population of salmon produced 1600 eggs per spawner, and egg to fry survival and fry to adult survival rates were 5% and 2.5%, respectively, the population would produce two recruits per spawner and could be harvested at 50%. The same stock, if placed in a hatchery with 90% egg to fry survival, would produce 36 recruits per spawner, and could be harvested at 97%. Table 2.4 shows how the sustainable harvest rate depends on the release to adult survival for a hatchery population with 1600 eggs per spawner and 90% egg to release survival.

Table 2.3 Maximum recruits per spawner for some Pacific salmon populations

Species	Number of stocks	Average maximum recruits per spawner	Exploitation rate at MSY (%)
Chinook	6	4.4	67
Chum	7	3.0	55
Pink	52	2.8	54
Sockeye	23	3.5	60

Included are Chinook (*O. tshawytscha*), chum (*O. keta*), pink (*O. gorbuscha*) and sockeye (*O. nerka*) salmon.

Table 2.4 Sustainable harvest rate for hatchery fish as function of smolt-to-adult survival

Ocean survival (%)	Sustainable harvest rate
0.08	0.13
0.10	0.31
0.50	0.86
1.00	0.93
2.00	0.97
3.00	0.98
5.00	0.99

An extensive tagging programme using coded wire tags since the 1970s has tagged tens of millions of hatchery fish each year in North America, allowing us to estimate the survival rate of hatchery fish for most hatcheries. Figure 2.20 shows the distribution of survival rates from hatchery released Chinook and coho salmon from this database. The average sustainable harvest rate for these three species is between 86% and 98%, far in excess of the sustainable harvest rate for wild stocks.

5.3.1. Sustainable harvest in mixed-stock fisheries

When SEPs are technologically successful, the stocks they produce can be harvested at very high rates, and this creates one of the primary problems in management of enhancement programmes. When natural stocks with lower

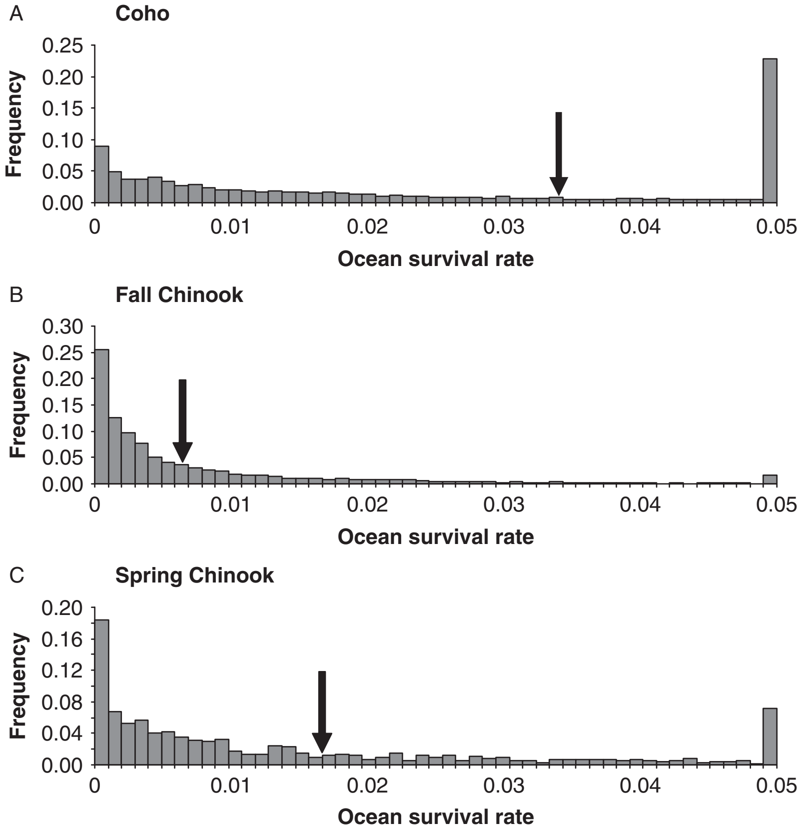

Figure 2.20 The frequency of ocean survival rates for hatchery release groups of coho (*O. kisutch*) (A), fall Chinook (B) and spring Chinook (C) (*O. tshawytscha*) from all hatchery releases in the Pacific salmon Coded Wire Tag database (Magnusson, 2002). The arrows show the average value for the salmon species.

sustainable exploitation rates are mixed in the same fisheries, how do you harvest the hatchery stocks without over-harvesting the naturally producing stocks? In theory, we would like to harvest each stock individually, be it wild or hatchery. In such an ideal world, this practise would allow us to harvest the hatchery stocks at very hard rates and the wild stocks at the appropriate rate. Unfortunately, two factors prevent this practise from happening.

First, for historical reasons, most salmon harvesting does not take place where the different stocks (natural and hatchery) are separated. This separation often takes place within a river system, since most enhancement facilities are located well above tidewater, and by tradition most commercial and recreational harvesting takes place in salt water. In the extreme of large river systems in North America such as the Sacramento, Columbia, Fraser, Skeena, Copper and Yukon, dozens (or hundreds) of discrete stocks are found in the watersheds, often diverging from one another at spawning grounds hundreds of miles upstream. A primary reason most commercial fisheries take place in salt water is that the quality of the flesh deteriorates as the fish enter freshwater, reducing their economic value. Thus, for commercial reasons, freshwater harvesting is very undesirable. It is an unfortunate fact of life that most salmon fisheries are to some extent mixed-stock fisheries, and the majority of enhanced salmon populations will be harvested with naturally producing fish when fishery enhancement takes place in a geographic region with natural production.

The problem of harvesting stocks of differential productivity in a common fishery is commonly called the 'mixed-stock harvesting problem', and has long been recognized and analysed (Hilborn, 1976, 1985b; Kope, 1992; Paulik *et al.*, 1967; Ricker, 1958; Shaklee *et al.*, 1999; Walters, 1988). Figure 2.21 shows the relationship between harvest rate and sustainable yield for a weak wild stock with potentially 1.5 recruits per spawner, and a stronger hatchery stock that produces 6 recruits to the fishery per spawner. Panel (A) shows the case where the wild stock has a potential return of 1000 spawners and the hatchery stock of 100. Fishing near the optimum rate for the wild stock (about 20%) maximizes the total harvest from the mix of stocks. However, if the hatchery is larger (panel B), its potential return is 600 spawners (still well below the potential return of the wild stock), and harvesting at about 70% maximizes the yield. This harvest rate is near the optimum for the hatchery stock but drives the wild stock extinct.

5.3.2. Salmon harvesting and impacts of hatchery fish on wild fish

Salmon fisheries can be broadly divided into two types: terminal fisheries near river mouths targeting fish as they return to a particular watershed, and mixed-stock or 'interception' fisheries that harvest a range of stocks that are intermingled. Most fisheries near the mouths of larger rivers are actually

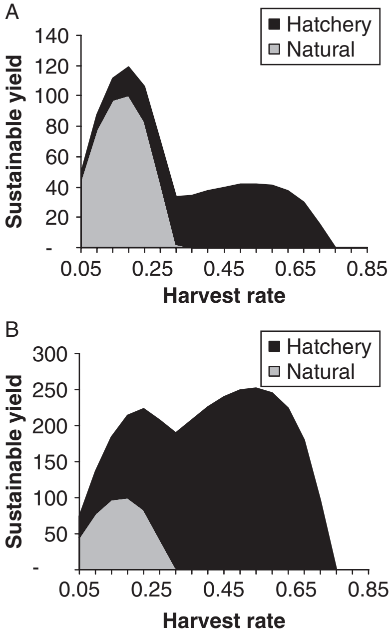

Figure 2.21 Total sustainable yield (TSY) for a fishery with a mix of a weak natural stock and a hatchery stock. TSY when (A) the hatchery stock is small ($N = 100$) relative to the wild stock ($N = 1000$) and (B) when the hatchery stock ($N = 600$) is just over half as large as the wild stock ($N = 1000$).

mixed-stock fisheries, since there is normally a range of stock complexes within any river system. But we generally do draw a contrast between the mixed-stock fisheries for immature Chinook and coho salmon that are highly intermingled along the west coast of North America, with the much more terminal (and less mixed) fisheries that take place in river mouths. Similar problems are found in the Atlantic, where many of the traditional fisheries take place on stocks of very mixed origin (Crozier *et al.*, 2004).

The Chinook fisheries are a very good illustration of the mixed-stock problem. Figure 2.22 shows the distribution of exploitation rates on Chinook salmon from four specific hatcheries: Robertson Creek, located on the west coast of Vancouver Island; Big Qualicum, located on the east coast of Vancouver Island in the Straight of Georgia; the Nisqually hatchery located in southern Puget sound and the Upriver Brights (URB) from a hatchery located on the Hanford Reach of the Columbia River. The fig. shows that the distribution of exploitation rates for different stocks differs spatially, with the Robertson Creek stock caught primarily in northern British Columbia and Alaska, the Big Qualicum and Nisqually stocks caught primarily in the more local sport and commercial fisheries of the interior waters of British

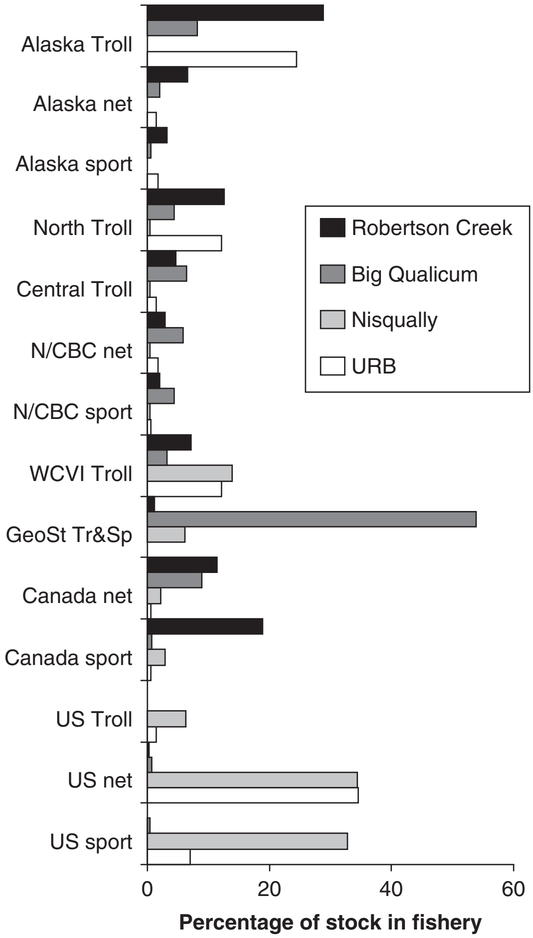

Figure 2.22 Distribution of Chinook salmon (*O. tshawytscha*) stocks in mixed-stock fisheries on the west coast of North America.

Columbia and Washington, while the URB stock is caught over most of the outer coast. Data suggest that wild stocks from the same geographic locations have similar distributions of catch, indicating that almost all of the major Chinook fisheries are heavily mixed. In other words, harvesters cannot put their lines or nets in the water without catching fish from many locations, including a mix of wild and hatchery fish.

It is these mixed-stock fisheries that pose the primary problem for wild stock managers faced with significant hatchery production. More importantly, the rise in hatchery production of Chinook and coho in the 1960–1980s led to high harvest rates in the coastwide fisheries that led, in turn, to over-harvest of the wild fish.

Figure 2.23 shows the historical pattern in exploitation rates on Big Qualicum hatchery Chinook as estimated from coded wire tagging data. Each year almost all hatchery stocks on the Pacific coast have a significant portion of their released fish tagged with small wire tags (coded wire tags), and catches and escapements are sampled to determine survival after release, harvest rates and stock contribution to mixed-stock fisheries. When the data became available, it was clear that the harvest rate on this stock was high, and indeed higher than that sustainable by wild fish (Pacific Salmon Commission Joint Chinook Technical Committee, 2002). The pattern observed for Big Qualicum hatchery fish was generally consistent with patterns of most wild Chinook stocks on the east coast of Vancouver island; that is, the harvest rates in the 1970s and 1980s were in excess of the sustainable rates for wild fish, and it was only in the 1990s that the harvest rates were reduced.

As we have seen (Section 3), most hatchery programmes on the west coast of North America have produced Chinook and coho salmon, the major exception being the recently established large programmes for pink salmon in PWS in Alaska (Hilborn and Eggers, 2000; Pinkerton, 1994). There are no fisheries for pink salmon outside of PWS, but the nature of the fisheries within this area is complex and there are significant concerns that the harvesting of hatchery fish has impacted the wild stocks. The nature of the geography and the migration of stocks have certainly posed significant concerns to the area managers. There is a tension between the desire of the managers to harvest the hatchery stocks as close as possible to the hatchery to reduce mixing with wild fish, and the economic desire to harvest the fish away from the hatcheries while the flesh quality is higher. Hilborn and Eggers (2000, 2001) showed that the advent of the large pink salmon hatchery programme in PWS coincided with a decline in the abundance and productivity of the wild fish at the same time that other wild pink salmon populations in Alaska were increasing. They suggested that the

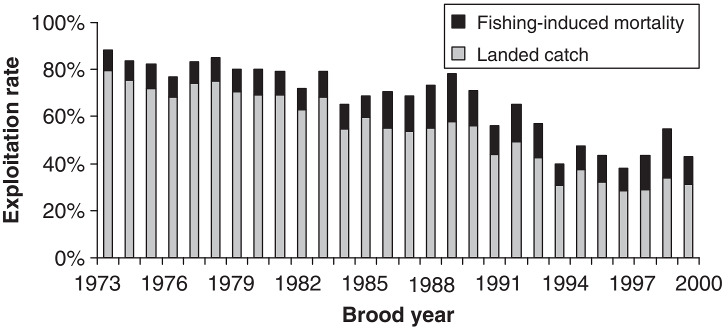

Figure 2.23 Historical exploitation rates on Chinook salmon (*O. tshawytscha*) from the Big Qualicum hatchery, British Columbia, from 1973 to 2000.

primary impact of the hatchery programme in PWS was to replace wild with hatchery fish rather than to significantly increase total pink salmon returns.

There is general agreement that fisheries agencies, in their desire to maximize the harvest of wild fish, systematically overfished many wild stocks, which led to the development of wild fish policies in Oregon and Washington in the 1990s. In 1997, the environmental impact statement for the Washington Department of Fish and Wildlife's Wild Salmonid Policy stated bluntly that 'current fish management plans and practices overfish 89 wild stocks in order to harvest co-mingled hatchery fish at rates that are not sustainable by wild populations' (Washington Department of Fish and Wildlife, 1997). This problem was not at all unique to Washington and has been found in every salmon jurisdiction that has had significant hatchery production.

5.3.3. Selective harvesting

Possible solutions to the mixed-stock harvesting problem include (1) continuing the overexploitation of wild stocks and relying on hatchery production, (2) closing of hatcheries, (3) reducing mixed-stock fishery exploitation rates to levels sustainable by wild stocks and (4) attempting to selectively harvest hatchery fish, in many cases by permitting fishermen to retain only hatchery fish (Lawson and Sampson, 1996; Zhou, 2002). Management agencies on the west coast of North America have mostly chosen to reduce exploitation rates while trying to selectively harvest hatchery fish at the same time. Selective fishing relies primarily on marking hatchery fish and encouraging fishermen to release unmarked fish, often by law. Thus, in some jurisdictions, all hatchery fish released have their adipose fin clipped and fishers can only retain adipose clipped fish. Selective fishing requires not only the ability to identify hatchery fish, but also that the survival rate of released fish is high.

5.3.4. Impacts of harvest: Summary

When hatchery programmes first became successful at producing significant numbers of fish for harvesting, the harvest of wild fish in mixed-stock fisheries was a very serious threat to the viability of the wild stocks. In the 1990s, growing recognition of the problem, aided both by better data from marking programmes and increasing concern about wild fish, led to a significant change in harvest policies in the Atlantic and the Pacific. The adoption of formal policies for protection of wild salmon has led to dramatic reductions in harvest rates in mixed-stock fisheries that should allow wild stocks to rebound where their freshwater habitat remains suitable and ocean conditions are favourable. There remains much discussion and controversy over the ability of selective fishing to continue to harvest hatchery surpluses without adversely affecting wild stocks. It remains to be seen if these efforts will be successful and, should the results prove negative, whether society will respond accordingly by reducing or redirecting demand for harvestable fish.

5.4. Disease effects of salmonid enhancement

In a strict sense, disease can be defined as a departure from normal and may include alterations in histology, physiology, behaviour or function. Diseases may have either infectious (e.g., tuberculosis, hepatitis) or non-infectious (e.g., botulism, cystic fibrosis) causes. Although fish provide many interesting examples of disease resulting from non-infectious etiologies (Leatherland and Woo, 1998), for the purposes of this chapter we will not consider diseases of non-infectious origin because they typically are not transmissible between fish. Nevertheless, there is concern that hatchery practises can affect levels of non-infectious diseases among wild fish by amplifying diseases that have a genetic etiology (e.g., certain cancers) or by the release of chemicals or pollutants. As an example, the use of malachite green for control of fungus infections in hatchery fish has been largely discontinued in Europe and North America due to its demonstrated carcinogenicity and concern about its release into the environment via the hatchery effluent (Srivastava *et al.*, 2004).

Disease is a natural process and one of the factors (along with age and predation) that determines rates of population mortality. It is important to remember that infectious disease is a normal component of ecosystems and that all species live in association with a broad suite of pathogens. Nevertheless, the presence of a pathogen in nature does not inevitably lead to infection and, should infection occur, it does not inevitably lead to disease. Thus, infections of fish can be acute, subacute, chronic or unapparent, and the infected fish may die, recover or become long-term carriers.

Several factors control the disease process in both wild and cultured populations of fish. These factors rest with the host, the pathogen and the environment (Hedrick, 1998). For the host, factors might include the species, stock, age, immune status and nutritional state. For the pathogen, factors include virulence, number and strain. In a normal environment, most endemic pathogens are in a relatively balanced relationship with their natural hosts. Both innate and adaptive immune mechanisms help protect the host against endemic pathogens, although pathogens with a high rate of mutation (e.g., RNA viruses) can be described as being in an 'arms race' with the host immune system. Because fish live in close association with their environment, changing environmental factors can have important effects in altering the balance of the host–pathogen relationship. Such factors include the presence of stressors, adverse water quality and abnormal water temperatures. The anthropogenic and natural stressors that reduce resistance or exacerbate disease in wild fish are typically local, for example, hydroelectric dams, thermal effluents from power plants, contamination from mining or industrial activities and altered flows or water temperatures from natural causes or agricultural practises (Arkoosh *et al.*, 1991); however, global or large-scale effects may also cause changes in disease ecology (Kocan *et al.*, 2004).

5.4.1. Infectious diseases of salmonids

A wide variety of viruses, bacteria, parasites and fungi can cause disease in salmonids and for more detailed information the reader is referred to various fish health texts (e.g., Hoffman, 1999; Noga, 2000; Plumb, 1999; Roberts, 2001; Wolf, 1988; Woo, 1995; Woo and Bruno, 1998). While the initial exposure of a population to an exotic disease is often devastating (e.g., whirling disease in rainbow trout), differences in the host specificity, virulence and the nature of the resulting disease are frequently seen with different strains of endemic pathogens as well. For example, IHNV is endemic among a wide range of anadromous salmonids on the west coast of North America; however, significant genetic differences have been shown among the different strains of IHNV that infect sockeye salmon, Chinook salmon, and the rainbow and steelhead trout (Kurath *et al.*, 2003). This finding underscores the need for caution to avoid the translocation of both exotic pathogens and non-native strains of endemic pathogens with the movement of hatchery fish. In addition, there are significant differences in the innate resistance to a given pathogen among the various salmonid species (Nichols *et al.*, 2003; Vincent, 2002) and even among stocks of the same species (Vincent, 2002). Finally, differences in environmental conditions and other factors (e.g., strains of alternate hosts) can affect the distribution and ecology of disease in various geographic areas. An example is the difference in the severity of whirling disease among populations of naturally spawning rainbow trout in different regions of the United States (Kerans *et al.*, 2004).

5.4.2. Infectious diseases in wild and hatchery salmonids

Typically, the sources of pathogens that can infect fish are endemic among free-living, facultative pathogens in the aquatic environment (e.g., *Flavobacterium psychrophilum*, the causative agent of bacterial cold water disease) or from obligate pathogens that are maintained among reservoirs in free-ranging aquatic animals (e.g., *Renibacterium salmoninarum*, the causative agent of bacterial kidney disease). Except for a few specific instances where exotic pathogens have been introduced to a new area by the intentional movement of hatchery fish (see below), these natural sources and endemic reservoirs among wild fish are the origins for the infectious diseases that affect both wild and hatchery salmonids (Amos and Thomas, 2002; Anderson *et al.*, 2000; Mitchum and Sherman, 1981; Olivier, 2002).

Although infectious diseases are common in populations of wild salmonids, their effects are hard to observe (especially in the ocean) and difficult to study. Many infectious diseases in wild fish occur at chronic or relatively low levels unless a significant environmental stressor is present or the population reaches an abnormally large size. Disease outbreaks that have resulted in large-scale mortality events among wild fish have been documented for several marine fish species (Hedrick *et al.*, 2003; Rahimian and Thulin, 1996) and some populations of free-ranging salmonids (Williams and Amend, 1976). In some cases, these outbreaks have resulted in losses approaching 90% of the wild stock.

Not surprisingly, much of what we know about infectious diseases of salmonids comes from experience with captively reared fish, where disease outbreaks are easily observed and there is an incentive for action, and because, at least in some cases, various disease control options may be available. As a result, most research on infectious diseases of salmonids has focused on those infectious agents causing large economic losses at commercial aquaculture facilities or large impacts at salmonid hatcheries supporting state, tribal and federal fisheries programmes. This has led some to the incorrect, but common, perception that fish disease is a hatchery phenomenon.

In addition to being more easily observed, when infectious diseases occur among fish in hatcheries, they are frequently found to have a higher prevalence or intensity than among wild stocks, although exceptions have been noted (Elliott *et al.*, 1997). Hatchery fish may experience greater impacts from infectious diseases due to higher densities, higher levels of stress and poorer water quality leading to an increased level of susceptibility and lowered ability to recover from infection. Other reasons that outbreaks of disease are more commonly observed in hatcheries might include a lower level of genetic diversity in some cases, and the fact that hatcheries typically rear the most susceptible life stages of fish, especially fry and juveniles.

5.4.3. Disease risks associated with salmon hatchery programmes

While an important area of concern, there are but a few well-documented cases in which hatchery fish have been shown to affect directly the health or infectious disease status of wild stocks (McVicar, 1997). Nevertheless, this remains a considerable area of debate and a major source of scientific uncertainty requiring additional research. However, there are several potential mechanisms by which hatcheries could affect the disease status of wild stocks.

5.4.3.1. Introduction of exotic pathogens While principally associated with the intentional movement of cultured fish harbouring an undetected infectious agent, this remains the most dangerous and best-documented threat to the health of wild stocks. Often cited examples include the introduction and distribution of *M. cerebralis*, the causative agent of whirling disease, and *Gyrodactylus salaris*, the causative agent of gyrodatylosis. Both of these important salmonid diseases have impacted wild or free-ranging stocks, sometimes with devastating consequences.

Whirling disease was believed to have been initially introduced into cultured rainbow trout in the United States sometime in the 1950s either by direct importation of infected fish from Europe where the causative agent is endemic or by use of imported fish as trout food (Bartholomew and Reno, 2002). Now present in both captive and free-ranging salmonids in at least 23 states, the parasite continues to spread both by natural means and by the intentional or unintentional movement of infected fish by commercial farms and fisheries agencies. Among wild-spawning rainbow trout in the western United States, declines approaching 90% have been observed in certain populations (Baldwin *et al.*, 1998). Because several species of anadromous salmonids are highly susceptible, there is significant concern for wild stocks of Chinook salmon, sockeye salmon and steelhead trout in the western United States (Hedrick *et al.*, 2001).

G. salaris is a trematode parasite that is cited as having caused significant damage to wild Atlantic salmon populations in 44 Norwegian rivers (Peeler and Murray, 2004). Spread from endemic areas by the movement of infected fish used in commercial aquaculture (Johnsen and Jensen, 1986), the parasite is now present in many rivers in Norway with little chance of eradication.

While the greatest risk of introducing exotic pathogens is associated with the deliberate movement of infected fish between watersheds, other pathways have been postulated. These include birds, anglers, ballast water and straying fish (Bartholomew *et al.*, 2005; Peeler and Thrush, 2004). The operational plans of most conservation hatcheries preclude many of these risks because they rely on local stocks, have good fish health inspections and restrict the movement of fish to the same, or nearby, watersheds. Because fish pathogens are detected most readily when they affect stocks in hatcheries, it is common to assume that a newly discovered pathogen is a result of an introduction, however, this is frequently not true (Mork *et al.*, 2004).

5.4.3.2. Amplification of endemic pathogens in hatchery fish A second method by which hatcheries are assumed to impact the health status of wild stocks involves the creation of a point source of infection from disease outbreaks that occur in hatchery fish. Since hatcheries often contain high densities of susceptible fish, such outbreaks can result in the release of significant quantities of infectious agents in the effluent (Watanabe *et al.*, 1988); although high levels of pathogens can also be released from wild salmonids in natural systems (Mulcahy *et al.*, 1983). The threat to wild stocks from pathogens in hatchery effluents is related to the number and concentration of infectious units that are released, the dilution of the effluent by the receiving waters, the stability of the infectious agent in the environment and the opportunity to contact a susceptible wild fish. An example of this type of risk is the amplification of sea lice (*Lepeophtheirus salmonis*) by commercial Atlantic salmon farms in Europe and North America (Krkosek *et al.*, 2005; Morton *et al.*, 2004; Peeler and Murray, 2004; Tully *et al.*, 1999), and the dramatic collapse of sea trout stocks on the west coasts of Ireland and Scotland has been attributed to infection of post-smolts during their migration past such farms (Butler and Walker, 2006; Gargan *et al.*, 2006). However, others suggest that the role of commercial salmon farms in contributing to local infections is less clear and that infection pressure on wild fish depends on multiple factors (Brooks, 2005; Costelloe *et al.*, 1998). It should be noted that few, if any, examples are reported in which fishery enhancement or conservation hatcheries rearing Pacific salmon have been shown to amplify endemic pathogens in a manner that has resulted in an increase in disease prevalence or intensity among wild stocks in the watershed. However, because the same, or very closely related, strains of endemic pathogens infect both hatchery and wild stocks, it is currently difficult or even impossible to determine the origin of the infectious agent with certainty (Todd *et al.*, 2004). Nevertheless, a large hatchery operating on a small watershed that contains a substantial number of susceptible wild fish could present a source of risk to the wild cohort.

5.4.3.3. ***Intentional release of infected fish that contact wild stocks*** In addition to the release of pathogens in hatchery effluents, conservation hatcheries will typically release fish into systems at times or in ways that attempt to mimic the natural production cycles. In some cases, these captively reared fish may be undergoing a disease outbreak or harbouring pathogens that can result in a greater than normal risk of infection for the wild stock. While some fraction of naturally produced fish may also be infected with the same endemic pathogens, there may be times or circumstances when highly infected hatchery fish will be in close proximity with wild stocks having lower levels of infection. In such cases, concerns about disease transmission from hatchery to wild fish have been raised. One example is the possibility of increased disease transmission during barging of salmon around dams in the Columbia River, where both wild and hatchery-reared salmonids are held together in close proximity and in a relatively stressful environment during collection and transportation (Elliott *et al.*, 1997).

5.4.3.4. ***Reservoir for exposure of wild fish at abnormal times*** Another way in which a fishery enhancement or conservation hatchery might affect the health of wild fish is to serve as a long-term reservoir of infection. In this way, captive stocks that are chronically infected might continually release, albeit at low levels, pathogens that could initiate infections among wild fish during life stages in which they are most susceptible or do not normally encounter the pathogen in nature. For example, in western North America, IHNV is commonly found in spawning adult sockeye and is spread among these highly susceptible fish through the water where high levels of virus have been detected (Mulcahy *et al.*, 1983). Out-migrating fry are also highly susceptible to infection with IHNV, but by the time of fry emergence, adult carcasses have largely been removed from the system and the infection pressure on fry is low. A hatchery that provided a significant source of IHNV to the watershed at these times could have an adverse effect on this highly susceptible life stage in a manner not typical in nature.

5.4.3.5. Genetic effects of hatchery releases on disease resistance of wild stocks There are several methods by which hatchery operations could affect the innate disease resistance of wild stocks, including the stock or strain chosen for rearing in the hatchery. While less common at hatcheries using local stocks and exercising care to prevent inbreeding, stocks of hatchery fish having lower resistance to endemic pathogens could spread less favourable alleles at genes involved in resistance following interbreeding with wild fish (Currens *et al.*, 1997; Lawlor and Hutchings, 2004). This effect might be more likely for hatchery stocks having relatively modest differences in susceptibility compared to wild stocks because hatchery programmes choosing to rear and release stocks with significantly lower disease resistance than the wild stock have experienced very poor returns when such hatchery stocks undergo intense negative selection by endemic pathogens such as *Ceratomyxa shasta* (Bartholomew, 1998).

There is an increased effort to determine the genetic basis of disease resistance in fish. As an example, some alleles have been identified that are associated with increased resistance to IHNV, while others are associated with increased susceptibility (Miller *et al.*, 2004). Thus, even if local stocks are used, it is possible that hatcheries with highly effective disease control methods for endemic pathogens (e.g., a pathogen-free water supply) may provide a form of relaxed selection, leading to a greater frequency of alleles associated with susceptibility among the population of hatchery fish. If large numbers of these fish are released and do not encounter sufficient levels of infection in the wild, they can be expected to survive and return. If these hatchery fish are allowed to spawn with the wild stock, this relaxed selection might, over time, lower the overall resistance of the population.

While the genetic diversity of populations helps ensure survivors, hatchery diseases can exert intense selection. Some hatchery stocks that were founded from a natural population have been shown to have significantly greater resistance after a few generations of selection by disease (e.g., Chinook salmon in the Great Lakes). Such strong selection by one pathogen may be accompanied by a loss of resistance to a second pathogen (Hard *et al.*, 1992).

5.4.3.6. Release of unexposed stocks from hatcheries Hatcheries with effective disease control programmes and a source of pathogen-free water are able to rear and to release large numbers of uninfected fish. While this is generally assumed to be highly desirable, these unexposed fish may remain susceptible and could become infected with certain endemic pathogens following release. If large numbers of such fish suffer a significant disease outbreak while co-habiting with wild stocks (e.g., during barging operations), they could generate sufficient infection pressure to produce an added risk to the unexposed portion of the wild stock; although the magnitude of this risk is unknown. Such fish, infected later than their wild cohort, could also serve as carriers during in-river or ocean migration to infect portions of the wild stocks in areas where the disease is not endemic or at times at which it does not normally occur.

5.4.3.7. Introduction of pollutants or stressors that alter disease ecology A final method by which hatcheries could increase disease risk to wild stocks is by altering the ecology of a watershed. Naturally, this would be most likely for large hatcheries on small watersheds (Tervet, 1981). Effects could range from changes in stream temperature by large inputs of hatchery water, or phosphorous or organic matter that can increase algal growth or lower dissolved oxygen levels. Such stressors could be expected to affect the host–pathogen relationship for endemic diseases among wild fish.

Naturally, different types of hatcheries will show differing levels of these effects. In fact, each situation is probably unique. Compared with commercial aquaculture, conservation hatcheries can be expected to have significantly fewer of the most serious risks because they typically do not transport fish from outside the watershed and because they rear species, stocks and life stages that are usually derived from local, wild stocks. Nevertheless, additional research to assess the magnitude of these risks is needed.

5.4.4. Approaches to reduce effects of disease in hatcheries

Unlike their wild counterparts, there are many approaches that can be used to control the risk or reduce the severity of infectious diseases among hatchery fish. The choice, however, will depend to a significant degree on the type of facility involved. For example, disease control strategies that substantially increase overall costs tend to find few applications in commercial aquaculture but may be very appropriate for conservation hatcheries attempting to help recover threatened wild stocks. Hatcheries involved in recovery of local stocks are usually not involved with the movement of fish from distant watersheds and the associated risk of the introduction of exotic pathogens or new strains of existing pathogens. For these facilities, good fish health practises include good sanitation, sound nutrition, regular health examinations and disease monitoring (American Fisheries

Society, 2004; Winton, 2001). Further benefits can be achieved through reduction of stress by controlling fish density, water flow and temperature (Wedemeyer, 1998), and, when necessary, by careful application of drugs and chemicals (Stoskopf, 1993), vaccines (Leong and Fryer, 1993; Newman, 1993) or immunomodulators (Iwama and Nakanishi, 1996). Whenever possible, improvements to hatchery facilities should be a high priority, including using a pathogen-free water supply or disinfecting of incoming water (e.g., with ozone or ultraviolet light) and effluent treatment in some cases.

5.4.5. Application of risk assessment tools for disease management and control

In recent years, a topic of increasing interest is the application of the tools of risk assessment to the management and control of aquatic animal diseases (Bartholomew *et al.*, 2005; Office International des Epizooties, 2003). In addition to assessing the risk of the introduction, establishment and likelihood of adverse effects from the spread of a disease into a new geographic area via the movement of fish, the principles and methods of risk assessment can also be applied to help analyse ways to reduce disease risks for wild fish. While the reduction of disease in hatchery fish can lead to lowered risk for wild fish, the idea is not to simply compare the risks of hatcheries versus natural rearing, but to assess the various types and levels of risk posed by different strategies and to identify factors under management control that can affect risk.

5.4.6. Future work and knowledge gaps

As can be seen, there is considerable uncertainty surrounding many aspects of the disease risk posed by hatchery operations to wild stocks. Additional research or effort is needed in the following areas:

1. Improved methods for the detection of important salmonid pathogens (including non-lethal sampling techniques) and increased disease surveys of wild fish stocks to gain a better understanding of the distribution and level of these pathogens in nature. Additional work is also needed to validate these standard methods to ensure uniformity.
2. Studies to determine the host specificity and virulence of various strains of important viral, bacterial, protozoan and fungal pathogens affecting both wild and cultured salmonids.
3. Research to better understand the genetic basis of host resistance among salmonids and to map these traits on the salmonid genome in order to identify the genes involved in susceptibility and resistance. Genetic tools are needed to assess the levels of diversity required to maintain healthy populations, the heritability of resistance to infectious disease of salmonids and the genetic changes associated with the development of

resistance, domestication and interbreeding between hatchery and wild fish.

4. New information on the nature of the innate and adaptive immune systems of salmonids, including development of novel tools and assays to assess the factors that control the susceptibility of various species and strains of salmonids to various classes of pathogens.
5. Research to develop new vaccines to protect fish in hatcheries. This includes new-generation vaccines (e.g., DNA vaccines) and novel delivery methods.
6. Improved knowledge of the environmental factors that affect the ecology of infectious diseases of wild salmonids.
7. Improved and standardized legislation to prevent introduction, movement or spread of exotic pathogens and strains of endemic pathogens between watersheds.
8. Information on the risk to wild fish from the various types and levels of pathogens released from hatcheries. This includes studies on the pathogen shedding rate from infected fish, the environmental stability of the agent, effective dose/infection pressure that occurs in the wild and the transmission efficiency between fish in the wild.
9. Develop methods of risk reduction for various modifications in facilities or operations. These include effluent treatment, vaccination, disinfection, disease management and stress reduction. Apply risk analysis approaches to the introduction of exotic pathogens. Analyse and compare pathways and risks from aquaculture, ballast water, anglers, birds and other factors.

5.4.7. Conclusions

Infectious disease is an important component of the environment that affects both wild and cultured salmonids. Infections of salmonids may occur in watersheds, estuaries and the open ocean and, where stocks or species of wild and hatchery-reared salmonids overlap, many of the same pathogens will be shared by both. While hatchery operations can have impacts on the level of disease in wild fish that range from devastating (e.g., introduction of exotic pathogens) to inconsequential, the origin of infectious disease in hatcheries is nearly always from the aquatic environment itself or from reservoirs of infection that are maintained among free-ranging wild stocks. Additionally, the application of sound hatchery management practises and application of effective disease control strategies can do much to reduce the disease risk to wild stocks. This is especially true for conservation hatcheries where threats from introduction of exotic pathogens or different levels of disease resistance are lessened by the use of local stocks. Nevertheless, additional research is needed to provide information to better understand and quantify the risks to wild fish from infectious disease.

6. ECONOMIC PERSPECTIVES ON HATCHERY PROGRAMMES

Salmon enhancement efforts programmes absorb large amounts of economic resources, and they often claim to provide substantial benefits in terms of commercial fisheries harvest, recreational fishing or conservation benefits. Because hatcheries constitute but one means of conserving wild broodstocks, or enhancing fisheries, economic assessments typically focus on estimating their costs and benefits, or their cost-effectiveness. The result can help salmon enhancement planners to select projects that achieve substantial results at reasonable cost. Successful economic assessments require comprehensive information on programme costs, reliable and quantitative measures of outcomes achieved and a means of measuring the economic value of outcomes. The assembling of reliable and adequate information covering all programme dimensions is relatively rare. Consequently, this section cannot provide a comprehensive economic summary of worldwide salmon hatchery programmes. It will lay out the basic conceptual framework for an economic assessment, summarize a handful of economic studies and provide some insight into complicating factors that make conclusive economic assessments difficult in practise.

Each of the salmon hatchery types that have been described in Section 1 has a characteristic operational pattern, incurs costs associated with operations and, frequently, a blend of objectives. Figure 2.24 provides a useful scheme for evaluating hatcheries by type of operation, based on broodstock origin (hatchery origin, wild origin or permanent captive broodstock), release location, release objectives and location where the adult hatchery fish return to a fishery or spawning site, and provides a basis for economic analyses of the operations. Project outcomes can be measured in physical

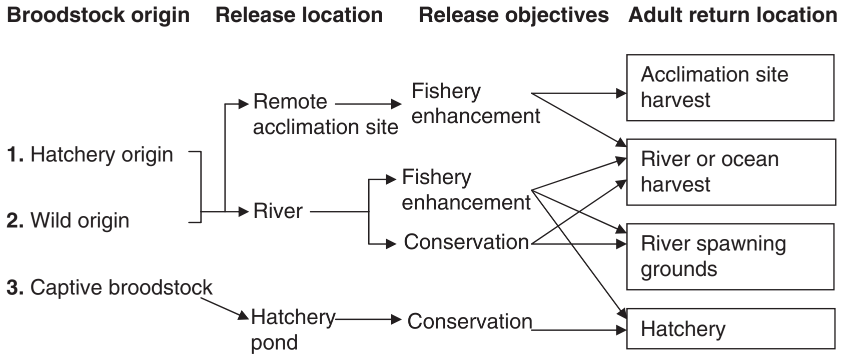

Figure 2.24 Depiction of various origins, handling routes and destinations for hatchery-spawned salmon.

terms (juveniles released, adult returns or size of broodstock preserved) as well as in economic terms (increased value of fisheries or benefits to the public). When enhancement projects are motivated by legal requirements or multi-purpose objectives that are not easily assigned an economic value, outcomes are expressed only in physical or biological units (e.g., number of returning spawners or increase in survival at some life stage). In such cases, it is useful to pursue cost-effectiveness analysis (CEA) of alternative projects or facility designs (see IEAB, 2002). The CEA reveals which projects provide the most performance for the cost incurred. When both project costs and economic benefit estimates are available, enhancement projects can be appraised via benefit-cost analysis (BCA). The BCA approach is most applicable for programmes that aim to augment or enhance fisheries or to establish or protect a salmon run with known value to people. To better inform policy makers, both BCA and CEA may need to be augmented by evaluation of other consequences such as regional employment or income impacts to account for broader socio-economic consequences (Fraser and Friedlander, 1980).

We could find few examples of economic analyses in Europe, and therefore we focus this discussion on SEPs in western North America. These programmes include private and public hatcheries that release juvenile fish for both enhancement of fisheries and conservation of wild stocks. For example, Wahle *et al.* (1974) and Wahle and Vreeland (1978) evaluated the Columbia River enhancement programmes, Boyce *et al.* (1993) assessed Alaska's salmon hatchery programme based on the increased economic value of the fisheries and Pearse (1994) evaluated costs and benefits of diverse projects in the salmon stock enhancement programme in British Columbia. In this chapter, we review some of these studies and comment on the use of economic evaluation of the hatchery and other enhancement facilities. Economic assessment methods can be applied to any form of salmon stock enhancement, including riparian habitat restoration and fish passage improvements (Paulsen and Wernstedt, 1995; Willis *et al.*, 1998; Wu *et al.*, 2000). Generally, an economic assessment is contingent on, and may be severely limited by, the availability of quantitative predictions of key biological outcomes of enhancement projects. Where the effects of enhancement projects on salmon populations cannot be quantified, an economic assessment may be premature.

6.1. Measuring costs, effectiveness and benefits

6.1.1. Costs

Project costs include both capital costs and annual operating costs. The capital costs comprise all initial and periodic investment expenses associated with planning, design, construction, equipment installation and replacement and land acquisition for the facilities. Operating costs involve salary and wages, personnel benefits, transportation, utilities and routine maintenance associated with the activities of trapping and holding adult spawners, hatching eggs, rearing fry and juveniles, maintaining water supply and quality, and research and monitoring. The costs are typically revealed in budget documents of the responsible agencies, but annual budgets often do not place expenditures in the accounting categories needed for economic analysis. Agencies rarely maintain accurate capital investment and depreciation accounts, and the lack of this information makes project assessment difficult. Also, administrative, monitoring and research costs are often assigned to separate offices rather than to individual hatchery operations. To provide an accurate synopsis of individual hatchery programmes, the costs that are shared among a number of hatcheries (often administration and research) need to be allocated on some basis to individual projects. To properly account for capital costs, both start-up costs and periodic maintenance or replacement costs of a facility need to be annualized over appropriate time spans. This is typically done by treating the capital cost as the principle on a loan, and calculating the annualized capital cost as equivalent to the payment required to pay off (or amortize) the loan over a specified period. For example, the capital cost could be annualized over a 30-year period with an annual interest rate of 5%. Annualizing the capital cost facilitates comparison of annual costs (operating and capital costs) with the value of the hatchery's contribution to the fishery.

The full costs may be assembled into a summary table, displayed in accounting categories (such as labour, materials, transportation, utilities, feed, maintenance, capital expense). Where costs for a large number of similar projects are available, the results may be a statistically derived functional relationship between total or component project costs and fish release numbers, fish species, hatchery type, location and other variables that influence costs (Loomis and Fix, 1999). The accounting display provides a detailed snapshot of a particular project (or class of projects), while the functional cost equation provides a means to forecast how costs vary with hatchery size or design.

6.1.2. Effectiveness

Effectiveness should be measured to reflect the main purpose, or purposes, of the enhancement project. A fishery enhancement hatchery could be judged by the magnitude of the run size increase or harvest contribution. A conservation hatchery might be judged by the magnitude of increase in a wild salmon population. To be a useful planning device, CEA must incorporate information from a range of alternative enhancement projects. If a fixed budget for enhancement were available, a cost-effective group of projects would be those that achieve the most effectiveness for the budget. On the other hand, if a fixed enhancement objective were firmly established, the CEA would assist in selecting a mix of projects that achieves that objective at lowest cost—that is, a programme that meets the objective cost-effectively.

Measuring the contribution of a hatchery to the size of salmon populations is a difficult research task, involving tag release and recapture data, smolt-to-adult survival estimates, harvest rate estimates (often for several geographically separate and mixed-stock fisheries) and hatchery return and straying estimates. Further, where a hatchery brood interacts with wild stocks or other hatchery stocks (via competition for food and space, disease transmission or interbreeding and genetic modification), the contribution of the hatchery to run size and harvests must be adjusted to account for possible negative changes in the other stocks. When a hatchery depends on continued capture of natural spawners for broodstock, the net increase in run size attributed to the hatchery should reflect the hatchery-origin run minus any reduction in natural spawning run.

6.1.3. Benefit-cost analysis

BCA tackles the more complex task of estimating economic value of the project outcomes. For production hatcheries aimed at commercial fishing (e.g., the Alaska SEP), the benefit is simply the net economic value of increased fish harvests (i.e., sales value minus increased harvesting cost). Where recreational fisheries take some or all of the fish, recreation benefits can be assessed using recreational demand models based on the travel cost method (see Brown *et al.*, 1983) or one of the more sophisticated recreational choice models (see Berman *et al.*, 1997). Subsistence fishing, especially treaty-obligated fishing by Native peoples, presents a more difficult conceptual task that has, frankly, not been addressed adequately by salmon economics research. Further, people who appreciate the existence or preservation of unique salmon runs hold non-use values, which do not depend on harvesting fish. Non-use values can be assessed using actual or hypothetical payments in response to questions posed in surveys, using the contingent valuation method (see Bell *et al.*, 2003). In some circumstances, salmon enhancement projects may sometimes produce all four types of benefits—commercial, recreational, subsistence and non-use value—making the benefits assessment a challenge. Further, conservation hatcheries typically provide benefits through an increase in wild stocks, and all the types of economic benefits would be applicable to these as well.

6.2. Cost-effectiveness of hatchery programmes

Two recent attempts at CEA serve to illustrate the method and the complications associated with the method. The Northwest Power Planning Council's Independent Economic Analysis Board (IEAB, 2002) assessed cost-effectiveness of six hatchery programmes and one acclimation and release programme in the Columbia River Basin. The IEAB's objective was to provide advice regarding expenditures in the Council's Fish and Wildlife Programme, which spends roughly $40 M a year on salmon enhancement projects. The initial phase of that work studied five ongoing production hatcheries, including a lower river fall Chinook hatchery; an upper Snake River summer Chinook hatchery in Idaho; a multi-hatchery complex in the upper Columbia at Leavenworth, Washington; a steelhead hatchery in the mid-Columbia and a fall Chinook hatchery operated by a public utility district. The resulting short report and technical appendix (IEAB, 2002) were reviewed by the agencies and other technical staff. At about the same time, the Audits Division of Oregon's Secretary of State examined Oregon's hatchery programmes for cost-effectiveness. This study focused on 12 coho and Chinook hatcheries in western Oregon (Oregon Secretary of State, 2002). In both of these reports, each project was characterized by total releases, estimated smolt-to-adult survival, estimated total catch (all fisheries combined) and annualized costs. The costs are summarized in three forms: cost per fish (or pound) released, cost per adult survival and cost per adult caught. As with the BCAs discussed below, neither of these CEAs incorporates the effects of hatchery fish impacts on wild stocks.

An example of this type of economic analysis pertains to a salmon hatchery in McCall, Idaho, operated for fishery enhancement by the US Federal government. The hatchery rears summer Chinook in a facility with 2, large outdoor ponds, 14 indoor rearing tanks and incubation facilities. Initial construction costs in 1981 for the facilities were $5,453,000. Updating this fig. to 2000 by applying the US Gross National Product (GNP) price deflator yields a capital cost of $10,755,424. Annualizing this cost over 50 years at a 3% interest rate generates an estimated annual capital cost of $418,015. The costs and the production of smolts, the smolt-to-adult survival rates (SARs) and harvest rates were obtained for a 13-year period, brood years 1984–1997. The average cost per smolt released for that period was $1.09, the average cost per adult fish returning (to the fishery or the hatchery) was $271.80 and the cost per fish caught in the fishery was $1051.01. This cost occurred during a period of time when the salmon were experiencing relatively low ocean survival rates. The cost might be significantly lower during other periods of time.

The IEAB research results found that the costs per smolt (measured in 2001) varied from $0.08 for fall Chinook (sub-yearling smolts) released at a mid-Columbia public utility district hatchery to $2.60 for Chinook released as yearling smolts from the Nez Perce tribal hatchery. Based on both the data and discussions with hatchery managers, the IEAB found that the cost of producing sub-yearling smolts (fall Chinook) was substantially lower than cost per yearling smolts (spring and summer Chinook, steelhead, coho) for the obvious reason that the yearlings are reared and fed for a longer period. The cost per adult survivor ranged from a low of $12 for mid-Columbia fall Chinook to $3707 for spring and fall Chinook from the Nez Perce tribal hatchery. Again, the two lowest cost per adult estimates were for fall Chinook hatcheries. Finally, using estimated contribution rates to fisheries, the cost per adult fish caught ranged from a low of $23 for Priest Rapid fall Chinook to $68,031 for spring Chinook from an upper Columbia river hatchery on the Entiat River. The wide range of cost-effectiveness estimates suggest that reallocation of funds to better-performing facilities would offer an opportunity to achieve more harvest enhancement per dollar spent. On the other hand, the fig. for cost per harvest were the least reliable of the cost-effectiveness measures because the sampling of tags from in-river fisheries was of unknown accuracy. Further, the Nez Perce tribal hatchery has just begun production and has focused on supplementation (conservation) of local runs, not harvest per se. The objective of that programme is not simply to produce some fish for catch somewhere but to produce a particular sub-stock returning to a particular tributary. Hence, comparability across hatcheries is not as transparent as the numbers might suggest.

The Oregon cost-effectiveness audit found cost per pound of fish released to vary from $4.08 to $9.09 (measured in 2001); cost per adult survivor (hatchery return plus catch) ranged from $14 (Salmon River fall Chinook) to $530 (coastal coho at Bandon, Oregon) and cost per adult caught ranged from $27 (Salmon River fall Chinook) to $1442 (coastal coho at the Trask River). As with the Columbia Basin hatcheries, yearling releases are more expensive than sub-yearling releases, and the cost per fish caught depends strongly on both SAR and harvest rate. Harvest rates in Oregon salmon fisheries are geared to protect the weak stocks, and they have been tightly regulated in recent years to protect coastal coho and Columbia River Chinook stocks that are listed as threatened or endangered under the Endangered Species Act. Hence, a hatchery with a reasonably low cost per adult survivor may have a high cost per adult caught simply because their fish mix with protected wild fish and harvest rates are kept low. To change the locations or operations of hatcheries to improve the future harvest rate (and to lower the cost per catch) would require adapting to future fishing regulations that will respond to perceived depletion of various salmon runs with shorter fishing seasons and lower catches.

One way to lower the cost per fish caught would be to move the smolts from the hatchery location to an acclimation site away from protected stocks, with the intent of getting the fish to return to a site where they can be fished at a high rate. The Clatsop County Economic Development Council in Oregon funded a project of this sort starting in 1977 to enhance the lower Columbia River gillnet fishery. In recent years, this project has acclimated salmon in net pens in Young's Bay, west of Astoria (IEAB, 2002). The programme includes fall and spring Chinook and coho from various sources and fish are released at sites in the Columbia River estuary. The cost per fish caught from the programme range from $14 for coho to $233 per spring Chinook.

6.3. BCA of hatchery programmes

An early BCA of salmon hatcheries was conducted by the US National Marine Fisheries Service on the Columbia River Development Programme (Wahle and Vreeland, 1978; Wahle *et al.*, 1974). These studies were tied to very ambitious mark-recapture research efforts that provided estimates of hatchery contributions from 13 Chinook and 20 coho hatcheries to ocean and river fisheries. The ocean fisheries ranged from southeast Alaska to California, and the river fisheries include commercial gillnet, sport fishing and Native peoples' fishing. Total estimated contributions to coho harvests were 1.13 and 1.05 M fish for the 1965 and 1966 brood years, and contributions to Chinook harvests ranged from 11,000 to 602,000 fish for brood years 1963 through 1966. The capital costs (costs associated with design and construction of the facilities) were annualized over 30 years at a 3.5% interest rate. Operating costs were compiled for the spawning, hatching and rearing for two brood years of coho salmon (1965 and 1966) and four brood years for Chinook salmon (1963–1966). The commercial harvests were valued by multiplying the number of fish contributed to harvest, multiplied by the estimated weight per fish and the current ex-vessel price. Recreational harvests of coho were valued by dividing the economic value per angler day of $20 (estimated by Brown *et al.*, 1983) by catch per day and then multiplying by number of fish caught by sport fisheries. Recreational harvests of fall Chinook were valued at a straight $18.35 per fish.

Overall, Wahle *et al.* (1974) estimated economic benefits for the coho fisheries at $9.07 and $8.51 M for the two brood years. When compared to the coho hatchery costs of $1.29 and $1.23 M, the benefit-cost ratios were 7.4 and 6.6 for the 1965 and 1966 brood years, respectively. For the fall Chinook hatchery programme, annual estimated benefits ranged from $1.3 to $5.2 M, while the annual hatchery costs fell in a narrow range of $659,000–$748,000. Benefit-cost ratios for the fall Chinook hatcheries ranged from 2.0 for the 1962 brood year to 7.2 for the 1963 brood year, and had a 4-year average of 4.2. Of equal interest is the estimated variation in benefit-cost ratios for individual hatcheries that ranged from 11.2 for the Spring Creek hatchery to 0.3 for the Elokomin hatchery (1961 brood year only). In principle, reliable estimates of benefit-cost ratios for individual hatcheries, or even individual batches of fish within a hatchery, could be used to score and rank the underlying rearing regimes, locations and species. This information would feed into subsequent decisions regarding design and allocation of funds within the hatchery programme.

A drawback of these Columbia River hatchery studies is the use of ex-vessel price for economic value per pound of harvest. The logic for this procedure, outlined in Wahle *et al.* (1974), is that because the hatcheries are augmenting the harvest of an open access and economically inefficient fishery, the additional catch will add little or nothing to the harvesting cost.

Normally, economists would subtract additional harvesting cost from the additional catch, assuming that an increase in gross revenue from the fishery (especially in an open access fishery like the salmon fisheries of the 1960s) would attract additional fishing effort, thus increasing costs. Had this been done for these hatchery projects, the benefit-cost ratios would have been substantially lower.

The State of Alaska began a major SEP in the early 1970s, encompassing both state-run projects, under the new Division of Fisheries Rehabilitation Enhancement and Development (FRED) of Alaska Department of Fish and Game, and PNP hatcheries owned and operated by regional aquaculture associations (see also Section 5.3). During 1972–1992, the State appropriated $210.3 M to the new FRED division, and total expenditure by PNP hatcheries was just over $200 M (Boyce *et al.*, 1993). About 42% of PNP funds came from the State and the rest came from landings fees and cost-recovery fisheries. Cost-recovery fisheries, which are organized by the PNP hatchery associations, involve contract harvest for the association with sales revenue used to cover the costs of operating the hatcheries. In 1992, the Alaska State Senate sponsored the research reported by Boyce *et al.* (1993) in order to evaluate seven alternative actions being considered, including eliminating the pink and sockeye salmon hatcheries, and increasing or decreasing the two species' production levels by 15%.

The BCA analysis was approached using an Alaska accounting stance (Boyce *et al.*, 1993), that is, only costs and benefits accruing to Alaska fishermen, processors and agencies were counted. The authors used a biological model (Collie, 1993) to project catches by species and region over a 30-year time period. The prices for salmon under each alternative were computed from an international salmon market model (Herrman, 1993), and the benefits to the fishing industry were defined as the total revenue from sales of fish minus the costs of harvesting the fish. The net economic benefits to the State equal the benefits to fishers minus the costs of the enhancement programme. With these assumptions and estimates they estimated the following 30-year, statewide totals for the existing system (Alternative 1): total catch (includes all wild and hatchery fish), 353 million kilograms; gross revenue, $557 M; benefit to industry, $222 M; hatchery costs, $23.4 M and net benefits of $199 M to Alaska.

The main results were associated with Alternatives 2 and 3, which eliminated the pink and sockeye salmon enhancement facilities, respectively. For Alternative 2 (eliminating pink salmon hatcheries), gross revenues dropped by $5.5 M, industry benefits increased by $9.7 M, hatchery costs dropped by $6.4 M and Alaska net benefits increased by $16.1 M. The implied negative net benefit from pink salmon hatcheries occurred outside of PWS, where major pink salmon hatcheries generate benefits for the local fishery. Alternative 3 (eliminating sockeye hatcheries) reduced gross revenues by $8.75 M, increased industry benefits by $ 8 M, decreased hatchery costs by $4.1 M and caused an increase in state benefits of $12 M. Overall, this analysis suggested that Alaska would be better off economically without the pink salmon and sockeye salmon enhancement facilities. The report, however, warned that no recreational or subsistence fishing benefits were evaluated and that there may be some un-analysed strategic value to maintaining hatchery production to fend off the expanding salmon farming business in Europe and South America.

Canada's SEP in British Columbia was launched in 1977 with the objective of doubling salmon catches on Canada's Pacific coast through construction of hatcheries, spawning channels and other works. Over 17 years they spent $526 M, built more than 300 facilities and expanded the fish harvests by roughly 14,000 metric tons, or 13% of the annual salmon catch. This was somewhat of a disappointment, given the ambitious goal of the SEP. A very broad and creative BCA was performed by Peter Pearse for the DFO's Internal Audit and Evaluation Branch (Pearse, 1994). The Pearse report followed a series of previous evaluations by a Royal Commission, a Ministerial Task Force and three previous audits.

Pearse (1994) estimated the catch contributions, gross and net harvest values (for commercial, Native and recreational fishing) and lifetime costs (construction and operating) for the SEP facilities. The catch contribution due to SEP was estimated at 17,361 metric tons (50% chum, 19% sockeye, 10% pink, 12% coho and 9% Chinook). These contributions were not adjusted to account for interactions between hatchery and wild stocks because Pearse (1994) was unsuccessful at getting a consensus expert judgement on the extent of interactions. For the commercial fishery, net benefits were the sum of three pieces: vessel owner benefits (50% of gross revenue minus crew share), crew benefits (crew share minus estimated labour cost, valued at mean wage) and cannery benefits (50% of wholesale value minus fish costs minus variable costs of canning operation). The Native fishery benefits were valued at the 1993 ex-vessel price, with no deductions for harvest costs. The recreational fishery was valued by multiplying increased coho catch by $14 and increased Chinook catch by $54. Finally, Pearse (1994) used an 8% interest rate to value past costs and benefits as of 1993 and to discount future costs and benefits (out to 2017) back to 1993. Overall, the estimated present value of SEP in 1993 costs ($1.51 billion) exceeded the estimated net benefits ($919.9 M) by $592 M, leaving the programme with a benefit-cost ratio of 0.6. The benefit-cost ratios varied widely among enhancement projects; the spawning channels had a 2.2 benefit-cost and the lake fertilization projects a 1.3 benefit-cost ratio.

Pearse (1994) also provided a reasonable approach to additional decision making by dropping the past capital costs (the 'sunk' costs) and the benefits occurring before 1993. The result was an evaluation of the project from 1993 on, which is an important perspective for decision makers at that point in time. For this short-term decision framework, the benefit-cost ratio for the overall SEP programme rose to 1.6, with a net benefit of $165.3 M. In other words, given that the costs of investing in the facilities are irretrievable, there are net benefits to continuing the programme over the expected lifespan of the facilities. If we could go back in time to the programme start-up date, possessing the economic assessment produced in 1993, we might decide not to start the programme at all. Further, because the report contains specific estimated benefits for each major project, it is useful information for planning and adapting the content of the SEP.

6.4. Complicating factors

Several conditions add to the complexity and unreliability of SEP evaluations in practise. First and foremost, measuring programme effectiveness is absolutely reliant on biological and ecological modelling and analysis. As is evident from other sections of this chapter, the full impact of hatchery releases on aggregate run size depends on interactions among stocks, and particularly the effects of hatchery smolts on wild smolts and the effect of straying hatchery-origin spawners on natural spawning populations. These effects are often only roughly quantifiable and frequently controversial among experts. The economic studies reviewed above basically assume that the hatchery run represents a net increase in the volume of salmon returns from the ocean, despite evidence that this is not true in some cases (Hilborn and Eggers, 2001). A second complication is that large volumes of returns to hatcheries can affect market prices for salmon, at least within the region impacted and during the harvest season (Herrman, 1993). When the market price varies with the hatchery output, the economic benefits to consumers should be measured as the increased consumer surplus (i.e., the increased area under the estimated demand curve as the price falls). This measure requires additional research on the market demand for the salmon products.

A third complication is that enhancement projects can have a range of complex objectives that defy even concerted attempts at quantification. Experimental and research hatcheries focused on supplementation of endangered populations that may contribute to the long-term survival of listed species. While economists have estimated non-use values for salmon protection and restoration (Bell *et al.*, 2003; Loomis, 1996), it remains difficult to attribute specific values to specific projects that protect narrow sub-populations with known levels of risk. Further, many of the hatcheries in the Columbia River Basin were authorized in conjunction with multi-purpose river development projects (hydropower dams and irrigation projects). The construction and operation of the hatcheries represent a portion of the multi-purpose project objective to preserve some specific salmon or steelhead runs in the affected tributaries. Some observers note that the associated costs are attributable to the other project objectives, and that the trade-offs made in designing and authorizing the projects should not be recalculated later based solely on the performance of the hatcheries. There is necessarily a political balancing and negotiating aspect to these decisions that is not transparent in the economic analysis. Hence, the most that can be claimed for the economic assessment is that it is useful information for decision making when trade-offs among quantifiable objectives are being weighed.

6.5. Conclusions

Given the size and costs of public salmon hatchery-release programmes, careful and extensive benefit-cost and cost-effectiveness analyses would appear to have a useful role in salmon enhancement project selection and programme design. US Federal and State laws require that new programmes be evaluated for both environmental and economic consequences. However, salmon hatchery programmes have generally not been subjected to standard benefit-cost or cost-effectiveness analyses. Salmon hatcheries in the Pacific Northwest, British Columbia and Alaska are justified on other diverse grounds such as: (1) to mitigate for loss of spawning/rearing habitat, (2) to meet requirements of treaties, (3) to compensate for destruction of a natural salmon run via dam construction, (4) to augment commercial or recreational fishing and (5) to support threatened or endangered stocks. Only the short-lived commercial 'salmon ranching' operations in Oregon had the simple economic objective of producing harvestable fish that could sell for more than the cost of production. Hence, it is not surprising that the standard economic project evaluation techniques are rarely aimed at public salmon hatchery programmes. Nevertheless, it is also clear that SEP decisions strongly influence the magnitude of economic costs and benefits and that these decisions need not be made in ignorance of the economic consequences. The benefit-cost and cost-effectiveness analyses reviewed in this chapter show that a moderate research effort, using information normally collected for hatchery fish monitoring and budgetary purposes, can provide a reasonably constructed economic assessment of SEPs.

7. DISCUSSION

This chapter joins a growing number of papers that attempt to collate information on enhancement activities (National Research Council, 1996) and to evaluate the available evidence for the biological effects of such activities. We have presented the historical context and political underpinnings of hatchery programmes, reviewed the current level of releases from hatchery facilities in the North Pacific and Atlantic, discussed possible outcomes of interactions between hatchery and wild fish and have evaluated economic issues associated with the design and running of hatchery programmes.

Broadly, our chapter points to three major issues. First, decisions to initiate or sustain hatchery programmes are typically motivated by political objectives, which are rooted in historical contexts. These decisions are infrequently revisited and are rarely driven by biological or ecological reasoning. A holistic view of the effects of the production of salmonids on the ecosystem has not, in most cases, been taken into consideration. Rather, the effects have tended to be viewed in isolation. Second, there remains a dearth of information on the consequences of interactions between wild and hatchery fish despite the fact that hatchery programmes have been operating for since the nineteenth century. Third, the outcomes of hatchery releases and management steps are not fully understood because robust, systematic and coordinated scientific assessments are rare.

Such broad statements, of course, are only constructive when key gaps in the state of knowledge are identified, and placed in context of the objectives of conservation and fishery-enhancement hatchery programmes. We attempt this task here, while acknowledging that reviewers examining the same data sets often reach different conclusions (e.g., Brannon *et al.*, 2004a; Myers *et al.*, 2004). Nevertheless, recent political events have motivated individual scientists and advisory groups to formulate guidelines for the management of these types of hatcheries (Mobrand *et al.*, 2005; Waples and Drake, 2005), and we examine below some of these guidelines in the context of our assessment of the major knowledge gaps in the field.

7.1. Release objectives and release sizes

We initiated the review by providing a classification system for enhancement activities in recognition of the fact that differing objectives for hatchery programmes would lead to a range of biological outcomes. We then pointed out that these objectives have rarely been identified and subsequently enacted upon (Section 4). Without these defining objectives, individual programmes cannot be held accountable if they do not have a clear set of measurable guidelines. The same issue has been raised by a number of authors (Waples and Drake, 2005; Waples *et al.*, 2007), and has been identified as a key guiding principle in formulating recommendations for hatchery programme reform (Mobrand *et al.*, 2005).

We noted an absence of standardized approaches towards the collection and archiving of data on hatchery release sizes. This outcome is not surprising since hatchery activities are defined by political boundaries. We also noted that data quality varied across the countries we surveyed. Reporting would be most useful to the scientific community if the release goals of hatchery programmes were clearly identified and if attempts were made by the international community to centralize release data in a readily accessible format. The effects of hatchery programmes likely transcend watersheds and international boundaries and the development of a clear understanding of the extent of these effects would be well served by the collation of large data sets. It is particularly important to identify the relevant scale at which this data should be collected. Ideally, data sets should be collated hierarchically; levels of production and survivorship should be reported at the freshwater, estuarine and oceanic stages. Hierarchical data sets will be valuable for identifying the relevant scales over which interactions between hatchery and wild fish should be appraised. Finally, we noted that the effects of hatchery releases on the ecosystem were difficult to evaluate because of the paucity of data collected at this level.

7.2. Interactions between hatchery and wild fish

The literature on interactions between wild and hatchery fish was examined by exploring genetic effects, competition, harvest interactions and disease transmission. We acknowledged that this list was incomplete, but we also noted that there have been few concerted experimental approaches to understanding the outcomes of these interactions.

7.2.1. Genetic issues

Most examples of the genetic interactions between hatchery and wild fish have been retrospective and case specific, and have rarely been defined in terms of their release goals. While these studies point to a frequent outcome—that releases are often detrimental or unsuccessful—there is still a strong need to gain an understanding of the degree of risk posed by hatchery fish, and whether these risks can be reduced by correct management. Recent experimentation and a change in philosophy towards solution-based research appear promising. Part of the problem associated with research in this area is that most experiments require several generations of returning adults, and the resources needed to complete such experiments have seldom been available.

Relatively new guidelines have been presented by a scientific advisory group in the Pacific Northwest (Mobrand *et al.*, 2005). One recommendation aimed at reducing genetic impacts is that hatchery broodstock be either integrated with, or segregated from, wild populations (Mobrand *et al.*, 2005). This guideline is based on theoretical treatments that examined changes in fitness traits with varying levels of migration between hatchery and wild fish (reviewed in Section 5.1; modified from the model proposed by Ford, 2002), and is aimed at preventing the negative outcomes of reproduction between wild fish and hatchery fish that have been subject to domestication selection. The authors also point out that issues such as genetic drift, inbreeding, changes in effective size (the Ryman–Laikre effect) and outbreeding depression might be reduced by correct management of broodstock collection, mating and rearing protocols and individuals released (Section 5.1; see also Waples and Drake, 2005).

The recommendations of Mobrand *et al.* (2005) promote active management approaches rather than risk-averse measures, and will likely be debated in the scientific community over the next few years. For example, it has been noted that the impact of an integrated release on a fine scale metapopulation structure is unknown (Utter, 2004), especially if the other components are demographically unstable. It is also uncertain whether hatchery fish may be practically segregated from spawning wild fish once they have been released to the wild, although it has been argued that domesticated, less fit individuals might pose lower risks (Utter, 2004). Discussion on new management approaches are likely to be lively in the coming years, but recommendations such as those proposed by Mobrand *et al.* (2005) provide a framework for future experimentation on 'problem solving' approaches, and such research is strongly supported here.

It is quite clear that genetic issues have been placed at the heart of the 'hatchery-wild' debate. If one concern has been identified in this chapter, it is that many hatchery programmes continue to be operated with few objectives, and with a poor understanding of the magnitude and importance of the impacts of genetic effects of hatchery releases and the role of this information in informing remedial actions. The field has been invigorated by recent hatchery reform initiatives, but management recommendations that are implemented broadly without an experimental approach and without identifying long-term goals will continue to perpetuate this problem, possibly with the negative consequences that have been widely reported to date.

7.2.2. Competition

We identified two key assumptions that are embedded in the philosophy underlying hatchery operations. The first assumes that captive rearing is appropriately directed at the most limiting life history stage. For many species, this limitation is not at the egg to smolt stage at which most operations are directed, but during the juvenile rearing period in freshwater streams or perhaps during their estuarine or early ocean stage. The second assumption is that competition between hatchery fish and their wild counterparts does not counteract the aims of the hatchery programmes. If, as was pointed out, the carrying capacity of the environment is limited (and this has been demonstrated in a broad range of studies in freshwater and a limited number in estuarine and marine environments), then competitive interactions between the two components can have negative outcomes.

The nature and level of behavioural interactions between hatchery and wild fish may vary with the type of hatchery programme. If conservation-based hatcheries are considered first, then the primary aim of recovering a threatened population would be best served by producing hatchery fish whose distribution in physical form and life history characters (and, by implication, in genetic composition) does not differ from that of their wild counterparts. The simple notion would be that competitive interactions would not favour one component over the other. However, many programmes have been established to recover weakened populations without considering the underlying causes of the population decline, and specifically, which element of the habitat has proven limiting. Thus, releases of wild-type hatchery fish under this scenario may not result in the intended demographic boost if the original limitation is not addressed. Hatchery fish released for fisheries augmentation may differ from wild fish in a number of physical and life history traits and may differ in abundance. These differences can have complex outcomes, depending on the extent of spatial and temporal overlap between hatchery and wild fish.

Practically, authors have suggested that negative behavioural interactions can be avoided in a number of ways that depend on the nature of the hatchery programme (Mobrand *et al.*, 2005; Waples and Drake, 2005). If the aim is to segregate the hatchery fish from the wild, then interactions during early freshwater stages can be reduced by releasing smolts that migrate rapidly to sea or by producing larger smolts that utilize different habitats than the wild fish. Marine carrying capacity should factor into estimates of release size, although it is acknowledged that calculations based on this parameter are unlikely to be realistic over the short term and only relevant to changes in ocean regimes related to large-scale climate cycles (Mobrand *et al.*, 2005). Competition for spawning habitat may be eased by siting hatcheries away from spawning grounds and by maximizing imprinting to the hatchery itself. However, as was pointed out in Section 5.2, it is unclear to what degree competition and straying by hatchery fish on the spawning grounds can be alleviated by these measures, and generally, the locations of hatcheries are largely fixed.

While each of the approaches identified above may provide some solutions for segregated hatcheries, their utility is less clear for integrated hatcheries geared towards conservation because most of the steps will result in genetic differentiation between hatchery and wild components. For example, the release of fish larger than those found in the wild can be expected to change a suite of life history characters within the run, most notably age at maturity. The issue here is whether hatcheries can produce ‘wild-like’ fish in numbers that do not exceed the carrying capacity of the habitat and do not compromise the wild populations.

Our chapter collated a rapidly growing body of literature that points towards detrimental behavioural interactions between hatchery and wild fish. More is known about these interactions in freshwater rearing habitats than in estuarine and marine environments. There is also, however, a paucity of information on whether risk avoidance measures are effective at reducing competition and predation and, as far as we know, little attention is directed towards carrying capacity when the size of release is considered.

7.2.3. Harvest

The impact of harvest on wild populations becomes important when fishery-based hatcheries are considered. In theory, increasing the survival of a specific life history stage will support elevated harvest rates on the hatchery component of the population. The success of the programme will rely on the efficient segregation of the hatchery fish from the wild, which in turn is largely dependent on where and when the fish are harvested. Although two types of fisheries are recognized—terminal fisheries near the mouth of a river and interception fisheries in open waters—in practise, both target mixed stocks (although the former fishery likely comprises fewer populations than the latter). Commercial demand favours fishing at sea because flesh quality is higher during this life history phase. Ocean stocks do, of course, include a mixture of separate spawning populations, and overproduction of hatchery fish can lead to overexploitation of weaker stocks (often wild fish) within this mixture.

Several solutions to the 'mixed-stock harvesting problem' have been identified. The most controversial would lead to over-exploitation of the wild stocks and dependence on the hatchery component of the run for the persistence of the species, or almost as contentious, the termination of all production hatchery programmes. Most management agencies have instead relied on reducing exploitation rates to those sustainable by the weaker wild stocks and on selectively harvesting hatchery fish, which relies on efficient mass marking.

The success in setting appropriate exploitation rates depends on the accurate identification of a wild 'stock' so that appropriate forecasting and in-season management can be implemented. In Europe, it is recognized that the use of genetically isolated units within rivers is impracticable, and groupings based on populations experiencing similar abundance trends are being implemented instead in some places (Crozier *et al.*, 2004). Researchers monitoring mixed populations of Pacific salmon in the high seas often depend on genetic definitions of stocks (Beacham *et al.*, 2004; Seeb *et al.*, 2004).

Selective fishing requires that hatchery fish are accurately identified and that the survival rates of hatchery fish are high prior to harvest. Mass marking methods have, to a large degree, been successfully implemented in North America when the marks are clearly visible. However, the use of approaches such as otolith marking does not permit identification of hatchery fish until they are dead and, thus, they are of limited utility.

Several data sources point towards mixed success in consistently producing hatchery fish with high survival rates. Shifts in ocean regimes and marine productivity affect these rates with unintended consequences. If survival rates are low, then fisheries may inadvertently be redirected towards vulnerable wild stocks. On the other hand, excess fish escaping the fishery in a productive year can return to the spawning grounds, raising heated debates about the fate of those individuals (ISAB, 2002). In this case, interest groups have argued that returning hatchery fish can augment declining wild populations, but this view ignores the negative outcomes that are the subject of this chapter. Regardless, social dimensions often intervene, and fish from production hatcheries have been allowed to spawn in the wild in the past (examples given in ISAB, 2002). Finally, to our knowledge, there are no studies evaluating whether selective harvesting has been effective in reducing harvest risks to wild populations, and research on this issue is needed.

7.2.4. Disease

Historical movement of infected fish or contaminated eggs and the practise of using raw, unpasteurized salmon viscera as fish food have contributed significantly to the introduction or spread of many fish pathogens. However, awareness of these issues, implementation of strategies to control infectious agents in hatcheries and development of standards and guidelines for movement of aquatic animals have done much to reduce the spread of pathogens and the impact of infectious disease (Winton, 2001). The more controversial aspect of the 'hatchery-wild' debate is around the role of hatchery fish in amplifying and/or transmitting *endemic* pathogens to susceptible wild populations. While this issue is often raised as a criticism against hatchery operations, very little is actually known about this specific source of risk to wild fish.

Our lack of understanding in this area is explained partly by the fact that standard methods have been developed for the detection of fish pathogens (American Fisheries Society, 2004; Office International des Epizooties, 2003), there are few published studies that have determined levels of pathogens in populations of wild fish or in environmental samples and fewer still that have tried to assess the risk that infected hatchery fish or contaminated hatchery effluents might pose to wild populations. Current methods for epidemiological strain typing of pathogens typically cannot distinguish hatchery from wild origin, and thus it has been difficult to demonstrate the direction of transmission for pathogens affecting both hatchery and wild fish. Similarly, there is a poor understanding of the factors that control the ecology of infectious disease among populations of wild fish, the likelihood that wild fish will develop disease following exposure to a pathogen under natural environmental conditions or the effect of disease on the survival of salmonids in either freshwater or marine environments. What is clear from the few examples given in Section 5.4 is that the disease interactions between hatchery and wild fish are complex and may be case-specific.

Several approaches for reducing disease risks to wild fish include the following hatchery practises: sound sanitation, routine screening of spawning adults for pathogens, disinfecting fertilized eggs, maintaining families separately to reduce horizontal transmission and frequent disease monitoring during the rearing period. Additionally, lower rearing densities and good nutrition can reduce stresses that exacerbate disease. Finally, hatchery water supplies should be from pathogen-free source and the hatchery effluent treated, wherever feasible. Many of these practises are in place at a wide range of hatcheries (Waples and Drake, 2005).

In summary, the role that hatchery fish play in affecting the disease ecology of wild salmonid populations is highly equivocal. Research focused on the factors controlling the disease cycle in wild fish is needed to assist in determining the risk, if any, that hatchery fish pose to their wild counterparts.

7.3. Economic issues

To adequately consider the economic consequences of SEPs, at least two lines of inquiry need to be pursued further. First, the standard project evaluation and selection tools—BCA and CEA—are designed to assist in setting priorities and choosing projects for funding. As noted earlier, these emphasize efficiency in decision making and proper balancing of government funding when outcomes are quantifiable and economic consequences can be measured. Our review of past BCA studies shows that public salmon hatchery programmes generate economic consequences from high to low in terms of a benefit-cost ratio. By applying BCA to the sub-parts of the British Columbia salmon fishery enhancement programme, Pearse (1994) found some elements with high benefit-cost ratios even though the programme as a whole performed poorly by this standard. This information should assist in the selection of fishery enhancement projects that yield positive economic benefits. Existing CEAs show that hatcheries in the Columbia basin and Oregon have widely varying costs, ranging from $23 to $68,031 per additional fish caught. Clearly, where projects aim to increase fish harvests, hatcheries achieving a lower cost per fish represent a better public investment in fishery enhancement.

Because these objectives for conservation hatcheries and mitigation hatcheries (e.g., fishing opportunities for Native Americans) are less easily quantified in economic terms, BCA is less relevant to selecting projects of this type. Still, CEA is an appropriate decision tool where a range of alternatives is being considered for species protection or fisheries enhancement. Second, the project selection process inevitably triggers shifts in locations of government facilities and expenditures, and these fuel local economic impacts. Hence, impacts on small, rural communities become a focus for government decisions when salmon enhancement projects are being considered. This brings the discussion of hatchery openings and closing directly into the political crossfire as those most likely to be affected raise their concerns through democratic processes. Overall, since little economic analysis has been included in the design and project selection process for SEPs, it is not surprising that these programmes are not demonstrated to be strong contributors to our economic prosperity. Inclusion of improved economic analysis in project design and selection could improve the situation.

7.4. Moving forward: Scientific and social dimensions

Most enhancement activities are operated under the principle of 'adaptive management' (Section 3), that is, that hatchery practises should change as new scientific information becomes available. Practically, attempts to address many of the knowledge gaps we identify in our review have only recently been implemented and thus hatcheries have been slow to reform. We note, too, that there has rarely been a coordinated and programmatic approach to managing hatcheries within a given region. Throughout this chapter, it has been difficult to identify whether hatchery risks are due to inherent biological problems or due to poor management decisions. This criticism is not new (Hilborn, 1992a; Rich, 1922). Rarely have programmes been set up to effectively track any question, and, although a difficult goal to fulfil, they have not generated sufficiently systematic data to prove success or failure.

In some cases, political developments have led to a growing number of attempts to reform hatchery practises. We mentioned earlier that an independent scientific panel was mandated to review hatchery programmes in the Pacific Northwest and provide broad recommendations and guidelines for reforming existing hatcheries (Mobrand *et al.*, 2005). The process identified several key guiding principles that the nature and objectives of hatchery programmes must be clearly identified and programme success be measured against these goals, that operations and establishment of programmes should be scientifically defensible and that hatcheries should respond rapidly to new information as it becomes available.

While few people will quibble with such clear recommendations based on scientific principles, it is important to consider the social and political contexts in which the recommendations were made (Section 1). The reader is reminded of the arguments presented on the political aspects underpinning hatcheries (Section 3); namely that it is not science, but economic and cultural issues that motivate hatchery programmes. The hatchery reform process inherently acknowledges *a priori* that hatcheries have a role to play in recovering threatened populations or in enhancing fisheries, and it is in this political framework that the science is conducted. The alternative, that all hatcheries be closed, is unlikely to be seriously considered in the near future.

Thus, the successful implementation of any scientific approach is dependent on sustained political support.

Recent attempts to reform hatchery practises are a positive move. However, if the political process does not include ongoing attempts to answer the key knowledge gaps (some of which are identified above) then hatchery management will not have the appropriate tools for long-term monitoring and will continue to be managed without a sound scientific foundation. Without these tools, the larger question of whether hatcheries can, in fact, support conservation and harvest activities while minimizing risks to wild populations in a socially acceptable framework will remain largely unanswered. (This is not a trivial question: the counting of hatchery fish in listing decisions under the Endangered Species Act has been debated in court, and has resulted in policy reformulations in the United States; *Alsea Valley Alliance v. Evans; NOAA Federal Register June 2005.*) It should be noted, too, that the reform process attempts to change the practises of existing programmes and should not be interpreted as an excuse for creating new ones. Yet this is a possible outcome. The social and economic processes driving hatchery reform will inevitably use different measures of success than will biological approaches, and the formulation of a set of recommendations may be seen as that success. It should be emphasized that the reform of hatchery practises inevitably involves trade-offs between different risks (e.g., reducing competition between hatchery and wild fish in freshwater by releasing hatchery fish at outmigration may increase genetic changes due to domestication; Waples and Drake, 2005). The weighting of these risks will likely occur at the societal level. Finally, it should be noted that the implementation of hatchery reform is limited to the regions of the world in which the tenor of the political debate is at its strongest. It is still unclear whether there is sufficient social impetus to implement such changes worldwide, and yet it is clear that they are needed.

7.5. Conclusions

We conclude by restating the intent of this chapter. The subject matter has focused largely on areas in which hatcheries could adversely impact wild stocks. We do not suggest that hatcheries should not have a role in salmon enhancement where their use represents an important means to recover critically endangered stocks. In Section 1, we list several populations (e.g., the Snake River Sockeye in the Pacific Northwest) that would be extinct without a captive propagation programme.

However throughout this chapter, it has been difficult to separate biological factors from social factors in problems associated with salmon hatchery programmes. Despite the fact that hatcheries have been operated over many decades, it is still unclear whether such activities can support conservation and fishery goals. A greater emphasis should be placed on experimental approaches to reforming hatchery practises by conducting coordinated research within the existing and extensive hatchery system using appropriate controls. This research should be supported by a climate of active debate about the role of salmon hatcheries in today's society.

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THE SOCIAL STRUCTURE AND STRATEGIES OF DELPHINIDS: PREDICTIONS BASED ON AN ECOLOGICAL FRAMEWORK

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Abstract

Dolphins live in complex social groupings with a wide variety of social strategies. In this chapter we investigate the role that differing habitats and ecological conditions have played in the evolution of delphinid social strategies. We propose a conceptual framework for understanding natural patterns of delphinid social structure in which the spatial and temporal predictability of resources influences the ranging patterns of individuals and communities.

The framework predicts that when resources are spatially and temporally predictable, dolphins should remain resident in relatively small areas. Predictable resources are often found in complex inshore environments where dolphins may hide from predators or avoid areas with high predator density. Additionally, available food resources may limit group size. Thus, we predict that there are few benefits to forming large groups and potentially many benefits to being solitary or in small groups. Males may be able to sequester solitary females, controlling mating opportunities. Observations of inshore populations of bottlenose dolphins (*Tursiops* sp.) and island-associated spinner dolphins (*Stenella longirostris*) seem to fit this pattern well, along with forest-dwelling African antelope and primates such as vervets (*Cercopithicus aethiops*), baboons (*Papio* sp.), macaques (*Macaca* sp.) and chimpanzees (*Pan troglodytes*).

In contrast, the framework predicts that when resources such as food are unpredictable, individuals must range further to find the necessary resources. Forming groups may be the only strategy available to avoid predation, especially in the open ocean. Larger home ranges are likely to support a greater number of individuals; however, prey is often sparsely distributed, which may act to reduce foraging competition. Cooperative foraging and herding of prey schools may be advantageous, potentially facilitating the formation of long-term bonds. Alternately, individuals may display many short-term affiliations. These large groups make it difficult for a male or a small group of males to sequester a female, and polygynandry is the most likely mating strategy. While it is difficult to study wide-ranging delphinids to examine these predictions, this ranging and behavioural pattern has been suggested for dusky dolphins (*Lagenorhynchus obscurus*), coastal bottlenose dolphins (*Tursiops* sp.) and mixed species of dolphins in the Eastern Tropical Pacific. These patterns also resemble the ranging and social strategies of open savannah African antelopes and desert-dwelling macropods.

Resource availability exists in a range of complex distributions and we predict that delphinid ranging patterns will also vary. At intermediate-ranging patterns, the framework predicts that individuals should form mid-sized groups balancing intra-group competition with predation protection. Humpback dolphins (*Sousa* sp.) appear to fit this pattern, with some site fidelity over relatively large ranges. They display fluid associations with other individuals. Predation pressure is not sufficiently high to cause large groups to form, and individuals probably reduce predation pressure more by hiding whenever possible. This pattern is likely to prevent the formation of long-term complex bonds. In contrast, killer whales (*Orcinus orca*) also display intermediate-ranging patterns, but have extremely strong social bonds within familial groups. Cooperative and altruistic behaviour in killer whales facilitate the formation of life-long bonds, similar to those observations in sperm whales (*Physeter macrocephalus*) and elephants (*Loxodonta africana*).

This conceptual framework remains largely untested, and for many species it is not currently possible to describe ranging behaviours, anti-predator tactics or social behaviour in sufficient detail for appropriate examination of these ideas. Few studies on dolphins have been conducted to explicitly test this type of framework; however, existing observations of delphinid social strategies and communities are used throughout this chapter to examine this framework. Additionally, we anticipate that the present framework may provide a starting point to test hypotheses regarding the evolution of social strategies of delphinids.

1. BIOLOGICAL PRESSURES ON SOCIAL STRATEGIES

Dolphins have intrigued human observers since at least the time of the ancient Greeks (e.g., Reynolds *et al.*, 2000), and this fascination has largely been due to their obvious sociality. The popular literature is filled with stories describing apparent intelligence, communicative abilities, acts of altruism and social interactions of dolphins. The scientific literature tends to be less effervescent; however, there are a growing number of studies investigating the social lives of dolphins (e.g., Baird and Whitehead, 2000; Connor and Norris, 1982; Connor *et al.*, 1999; Karczmarski *et al.*, 2005; Krützen *et al.*, 2003; Lusseau *et al.*, 2003; Mann *et al.*, 2000; Möller *et al.*, 2001; Slooten *et al.*, 1993; Smolker *et al.*, 1992; Würsig and Würsig, 1980).

The 36 recognized species in the family Delphinidae (Rice, 1998) are a diverse assemblage of species, ranging in size from the 45 kg, 1.2–1.4 m Hector's dolphin (*Cephalorhynchus hectori*; Slooten and Dawson, 1994) to the more than 5000 kg, 9.0 m male killer whale (*Orcinus orca*; Dahlheim and Heyning, 1999; Fig. 3.1). The ecological habitats of delphinids are equally diverse, with species such as the Irrawaddy dolphin (*Orcaella brevirostris*) and tucuxi (*Sotalia fluviatilis*) present thousands of kilometres up river from the

Figure 3.1 Delphinids range widely in adult body size. (A) Hector's dolphin *Cephalorhynchus hectori* is the smallest delphinid, while (B) the largest is the killer whale *Orcinus orca* (see text). Both are disruptively coloured, mainly dark above and light below. The killer whale has a large white eyespot and white lower jaw, probably both for conspecific communication in murky waters and for confusing intended prey. Killer whales are sexually dimorphic, with males larger and a very high erect, at times wavy (as here), dorsal fin. (Photos courtesy of M. Würsig, with permission.)

ocean (Arnold, 2002; da Silva and Best, 1994), while others such as the striped and Clymene dolphin (*Stenella coeruleoalba* and *Stenella clymene*) tend to occur thousands of kilometres from land in the open ocean (Perrin and Mead, 1994; Perrin *et al.*, 1994). The delphinids also display diversity in group size and social structure, as some species typically occur in small fluid groups (e.g., Hector's dolphins; Bräger, 1999; Slooten *et al.*, 1993), while others are in large fluid groups (i.e., Hawaiian spinner dolphins *Stenella longirostris*; Perrin and Gilpatrick, 1994) and still others occur in highly structured, permanent groups (i.e., resident killer whales; Baird, 2000).

Additionally, even within the same species there can be clear differences in diet, behaviour and social structuring of different groups (i.e., killer whales; Baird, 2000).

Recent studies of several toothed whale species have given insight into some of the forces leading to the evolution of sophisticated social groupings, but the picture is far from clear (Connor, 2000). The focus of this chapter is to investigate what has shaped the evolution of group living in delphinids, the social strategies seen within groups of dolphins and to compare them with other well-studied systems. In particular, we address the roles that differing habitat and ecology have played in the evolution of social strategies. Research into the ecological basis of the evolution of social structuring of delphinids enhances our understanding of delphinid biology and conservation as well as provides insight into the evolution of complex social structuring in all mammals.

1.1. Why do animals form groups?

Animals form groups when survival and reproductive success of an individual is enhanced by group living. There are three major reasons individuals form groups: (1) when susceptibility to predation is reduced by group living, (2) when access to resources is increased by group living, and (3) when distribution of resources promotes gregariousness; for example, when there are only a few localized sites where resources such as water or shelter can be found (Alexander, 1974; Bertram, 1978). Once animals are grouped, then more sophisticated inter-animal social behaviours than sexual and nurturant interactions can evolve (Alexander, 1974).

Group living is a trade-off between competing factors. Potential benefits to group living include reduced predation, enhanced detection and capture of prey, increased acquisition or defence of resources, enhanced reproduction, reduction in parasitism and the possibility of social interaction and learning. However, group living can also result in increased predation, reduced foraging efficiency, increased competition for resources, reduced reproductive opportunities and increased transmission of parasites and disease. The matrix of cost–benefit ratios for an individual depends on its sex, reproductive state and ecology (Bertram, 1978). Costs and benefits to individuals are often measured in immediate returns such as rate of food intake or estimates of predation risk. However, it may be more appropriate to measure how group living and different social structures influence lifetime reproductive success, the number of surviving offspring an individual produces and even inclusive reproductive success, which not only includes individual surviving offspring but also considers shared genetic heritage passed on by surviving offspring of relatives (Lucas *et al.*, 1996). Such analyses are difficult, especially for long-lived animals, and even more so for marine mammals, where usually only a part of their lives can be traced when they are at the water surface.

The ecological basis for group formation has been studied extensively in terrestrial and aquatic environments (i.e., Beecham and Farnsworth, 1999; Bonabeau *et al.*, 1999; Wrangham and Rubenstein, 1986a), as have the correlations between environmental variables and group size (i.e., Arcese *et al.*, 1995; Baird and Dill, 1996; Janson and Goldsmith, 1995; Macdonald, 1983; Wrangham *et al.*, 1993). From this body of work, several overall themes emerge in relation to predation and foraging. In complex, highly structured environments, animals tend to be able to conceal themselves from predators, and group sizes are often smaller than in open habitats, or individuals may be predominantly solitary (i.e., Bednekoff and Lima, 1998; Brashares *et al.*, 2000; Wells *et al.*, 1999a). Diet specificity tends to increase competition between individuals and groups for limited resources, which in turn limits group size (i.e., Brashares *et al.*, 2000; Isbell, 1991). However, in certain situations, cooperative foraging and hunting can reduce the disadvantages of living in large groups (i.e., Creel and Creel, 1995).

When the advantages of group living outweigh the costs and animals live in groups, intra-group competition often occurs. However, when individuals within the group cooperate, competition can be repressed and cooperating groups out-compete non-cooperators (Frank, 2003). Thus, repression of competition can result in highly coordinated and cooperative groups, even when individuals are not related to each other. In fact, individuals in many cooperative groups are not related to each other and therefore kin selection cannot be used to explain these types of cooperation (e.g., Lukas *et al.*, 2005; Spong and Creel, 2004; Valsecchi *et al.*, 2002; Van Horn *et al.*, 2004; Vucetich *et al.*, 2004).

1.2. Definitions and levels of grouping

Although it may appear intuitive at first to define what constitutes a group of individuals, in practice this has proved more difficult and represents a rather contentious issue in the study of sociality. Some researchers define group to include all individuals occupying similar space at the same time; often expressed as a spatial scale (e.g., all individuals within 5 body lengths; Connor *et al.*, 2000b). However, this definition does not distinguish between individuals simply aggregated together, and those that share a common purpose. Other studies define a group to be all individuals in the same place at the same time, which are acting in a similar manner (e.g.,Connor *et al.*, 2000a). These definitions can describe aggregations and interactions that occur at a specific time, but do little to describe long-term patterns of association. Some studies define groups as individuals that spend proportionately more time together than with others (e.g., they are grouped if they spend 50% of their time together; Bigg *et al.*, 1990; Sailer and Gaulin, 1984). Additionally, primate and cetacean researchers have also used a variety of terms to denote grouping (e.g., subgroup, group, party, school and pod) and rarely are definitions consistent between studies. Therefore, it is essential to ascertain definitions used in each study before comparisons can be made between studies.

Five major groupings have been identified; and an individual animal can be considered to be in more than one at the same time. Population-level groups can be defined as all individuals sharing a common home range. Under this major level, feeding groups consist of individuals actively feeding on the same food resource at the same time. Foraging groups represent individuals that are searching or hunting for food together. Breeding groups include individuals that mate with each other (Gittleman, 1989). Nursery groups consist of mothers, their calves and at times their extended ‘other’ relations as well. Population level groups may split into subgroups for feeding, foraging, mating or nurturant activities, and then coalesce sometime later. In these situations, individuals may associate with a number of different individuals over time and relationships may appear rather fluid. These types of associations are often termed fission–fusion and are common in primates, cetaceans and some social carnivores (Connor *et al.*, 1998; Gittleman, 1989; Wrangham *et al.*, 1993). ‘Community’ refers to regional assemblage (society) of animals that share ranges, interact socially, but do not represent closed reproductive units (*sensu* Wells and Scott, 1999), which is similar to those in many primate studies (e.g., Boesch, 1996).

1.3. What are social strategies?

While extensive work has been carried out to examine the ecological basis for group formation and the relative advantages of various group sizes, relationships between individuals within groups can also vary with ecology and are an important aspect of group living. When animals are grouped in time and space, social behaviour can evolve, although this is not necessarily always the case (Alexander, 1974). If individuals only encounter each other once, then they do not have the potential to establish a knowledge base about the other individual. However, when associations persist over time, individuals can repeatedly come into contact with each other and establish a knowledge base of interactions (Hinde, 1976; Pusey and Packer, 1997). Such repeated interactions lead to the development of relationships (e.g., dominance, cooperative foraging and mating coalitions), and a description of the various relationships in the group can lead to a description of the social structure of the group (e.g., polygamous, female-bonded). Thus, the social structure of the group is based upon an abstraction of the nature, quality and patterning of relationships, and relationships are built upon a series of interactions between individuals (Hinde, 1976).

While social systems can be viewed as an abstraction of interactions between individuals, as well as the strategies that individuals employ when interacting with each other, the underlying behaviour of an individual is shaped by its ecology (i.e., distribution of risks and resources). However, the social organization and demographics of a group also place constraints on the behaviour of an individual, which create a feedback loop to the types of interactions between individuals and the resulting social structure (e.g., Kappeler and Van Schaik, 2002, and references therein).

1.3.1. Male versus female strategies

Social strategies vary not only with ecology but can also vary dramatically between the sexes. A female mammal transfers a large portion of her energetic resources to her offspring through lactation and gestation. Her reproductive success is limited by metabolic costs of lactation and gestation; therefore, a female may most effectively increase her reproductive success by investing heavily in each offspring. This is especially true for large mammals that typically produce a single offspring at a time. In contrast, male mammals often provide little parental care, and most effectively increase their reproductive success by maximizing the number of receptive females with whom they mate (Emlen and Oring, 1977; Wrangham and Rubenstein, 1986b).

This dichotomy between male and female strategies to increase reproductive success can lead to marked differences in distribution and social strategies (Ruckstuhl and Neuhaus, 2005). As a female tries to ensure the survival of each of her offspring, her distribution is often closely related to high-quality food resources and habitats that have lower risk of predation. The distribution of males, however, is often related more to female distribution than to availability of food resources (Emlen and Oring, 1977; Wrangham and Rubenstein, 1986b). Male strategies are especially tuned to the availability of reproductively active females, and can greatly be influenced by the length and synchronicity of periods of oestrus (e.g., Say *et al.*, 2001; Whitehead, 1990).

1.3.2. Mating systems

Among mammals, females are the limiting sex as they can only produce a restricted number of offspring in a single breeding season, while male reproductive success is limited by the number of females he can successfully monopolize (Emlen and Oring, 1977). Parental care by both males and females is required to raise offspring successfully in only a few mammalian species. In most mammals, females provide all the parental care, with little to no male assistance. In these situations, the ability of males to defend (from other males) a female, group of females, or a specific territory plays an important role in determining the mating system. If the core area where females range is defendable by a male or a group of males, then males are typically territorial, excluding other males from a specific geographic location. If females within this range are solitary or found in small groups, a single male may be able to defend the territory on his own. When females form larger groups, males may form coalitions to collectively defend the territory. Alternatively, when the core area where females range is not defendable, male territoriality is not observed. In situations where females form relatively stable groups, individual males or coalitions of males may exclude other males from accessing the group of females. If females are solitary or groups are widely dispersed, males may display a roving behaviour in which they search for receptive females and spend only short periods with each female. However, if females are found in unstable groups, males may form temporary mating territories or display lek behaviours during the breeding season. Thus, mammalian mating systems are often driven by male competition for access to females (Clutton-Brock, 1989), although female choice is likely to be an important aspect of mammalian mating systems, only recently being investigated. Male competition for access to females is especially important in delphinids, as females can only produce a single offspring at a time and have long interbirth intervals, for much of which time they may not be in oestrus (Whitehead and Mann, 2000).

Mating strategies have important implications for the dispersal of offspring. In almost all animal species, offspring of one sex disperse from the natal area, or both sexes will disperse. Mammals are predisposed for females to care for offspring, thus female philopatry is often favoured. For females, there may be advantages to staying in the natal area (or with the natal group), which can lead to the evolution of kin selection and altruism. Typically, male mammals then disperse to avoid inbreeding (Greenwood, 1980).

1.3.3. Evolution of social complexity and variability

Animal social complexity can be viewed as attempts by individuals to form cooperative solutions to challenges of survival and reproduction. In this framework, animal social systems can be described as alliances between individuals to simultaneously survive (find food, avoid predators) and reproduce (find a mate, mate and rear offspring), and alliance memberships and purpose may change with differing social and ecological conditions (Dunbar, 1989).

Social behaviour can be viewed as a flexible response that varies in relation to ecological and demographic factors. It is not possible to describe categorically the social organization of most species, as changes in physical and social environments of differing populations or communities may influence their social structure (Kappeler and Van Schaik, 2002). However, this does not preclude attempts to study social structure, or its evolution, as there will undoubtedly be several unifying themes in the evolution of social structure. Nevertheless, the focus should perhaps be on the investigation of these themes, rather than attempts to describe any one particular social structure of a species or subspecies.

1.4. How does ecology influence social strategies?

An individual's social strategy can clearly be influenced by its ecology. Resource and risk distribution are important factors (e.g., Cezilly and Benhamou, 1996; Geffen *et al.*, 1996; Johnson *et al.*, 2002), affecting social patterns and group size. Resource availability can vary both spatially (e.g., food patches that can occur in different areas such as mobile prey) and temporally (e.g., food patches that only occur at certain times of year such as fruiting trees). When resources are routinely available within a relatively small area, individuals (and groups) may remain resident in the area and in some situations can become territorial, defending their home range against the intrusion of others. When resources are highly variable over a range of scales, individuals must range widely and home ranges become very large and not defensible as exclusive territories.

Resource availability also influences the ways individuals interact as limited resources lead to competition. Scramble-type competition occurs when individuals (or groups) cannot exclude others from access to the resources and all individuals share equally in the resources (or lack thereof; Milinski and Parker, 1991). In this case, individuals (or groups) should distribute themselves such that they share resources equally (ideal free distribution; Fretwell and Lucas, 1970). Contest-type competition (also known as direct or interference competition) occurs when individuals (or groups) can exclude others from access to the resources (Milinski and Parker, 1991). Individuals or groups may establish territories, or simply defend the actual resource. In this situation, certain individuals (or groups) have greater access to resources than others. In groups with strong dominance hierarchies, or when individuals have great differences in competitive ability, one individual may monopolize all the resources, leaving all other members with none. The distribution and abundance of food resources usually determines the type of competition. Scramble-type competition tends to occur when the distribution of patches is homozygous and the patches are relatively small, or the patches are very large and indefensible. Contest-type competition tends to occur when patches are moderately sized and defendable (Milinski and Parker, 1991).

Residency rates and measurements of day range, that is, the linear movement of an individual or a group over a single day, can be used as proximate measures of resource availability and predictability. As large-scale movement may energetically be expensive or dangerous due to predation, individuals would be expected to range only as widely as needed to obtain required resources. Thus, individuals ranging widely are likely searching for dispersed resources. If competition between group members for resources is high, then group size is likely to be small, especially when resources are widely distributed, and for many species mean day range can be correlated with social grouping patterns (e.g., Wrangham *et al.*, 1993).

1.4.1. Special features of the marine environment

There are several features of the marine environment which have the potential to influence the relationships between a dolphin's ecology and its social structure. Dolphins live in a predominantly three-dimensional (3D) world, with many species having a large component of their daily movements in the vertical plane. It is unlikely that dolphins living in a strongly 3D environment such as the open ocean would be able to defend a territory, or even defend a large resource. It may be possible for individuals or groups to defend relatively small resources (such as a receptive female; see Connor *et al.*, 2000a), or for coastal dolphins to defend a territory, although this has not been reported (Connor, 2000; but see discussion of spinner dolphins, Section 3.2). Although dolphins may not often be able to defend territories, this deficiency may not incur the same costs as it would for territorial animals, as swimming dolphins appear to be able to increase their range of movements relatively easily, since the cost of locomotion is relatively low in marine mammals (see Williams, 1999, for details). Additionally, the marine environment is typically characterized by highly clumped and labile prey (Horwood and Cushing, 1978; Steele, 1985). Thus, contest-type competition may not be as important in the marine environment as it is in the terrestrial.

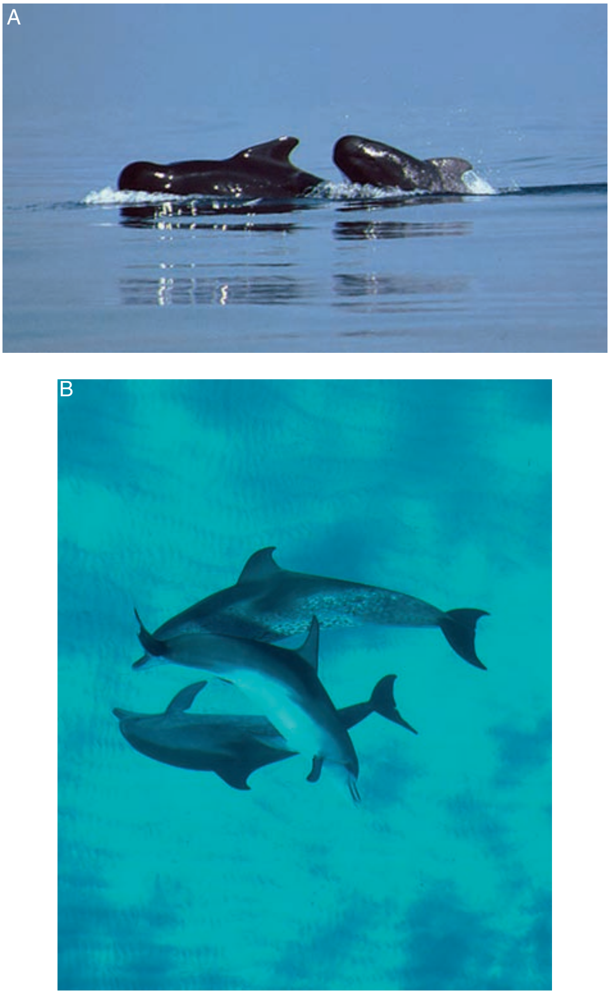
However, the 3D marine environment has implications for delphinid anti-predator strategies. In the open ocean, there are few if any places to hide and grouping may be the only effective anti-predatory strategy (Norris and Dohl, 1980). Additionally, the requirement of dolphins to routinely return to the surface to breathe further limits their anti-predator strategies.

2. DOLPHIN ECOLOGY

2.1. Distribution and habitat

Distributions of dolphins reflect a complex matrix of evolutionary history, phylogeny, prey distribution, predation risk, thermal tolerance and habit as learned from group members and ancestors. Some near-shore animals, such as *Cephalorhynchus* of the southern hemisphere, are more geographically restricted than many open ocean species that travel over relatively huge areas, such as common dolphins (*Delphinus* sp.), pilot whales (*Globicephala* sp.) and most species of the genus *Stenella* (Fig. 3.2).

Dolphins are found throughout the world's oceans and even into several large river systems. Broad habitat categorizations can be made, although there are subtle differences within these categories. While there is no consensus on exact habitat definitions, we use the following broad categories throughout this chapter. Riverine habitats consist of freshwater rivers and their brackish estuaries. Dolphins in these habitats can strongly be influenced by seasonal water levels and tidal cycle. Inshore habitats consist of protected bays, estuaries and tidal marshes. In these typically shallow-water habitats, dolphins can be influenced by tidal cycles and seasonal



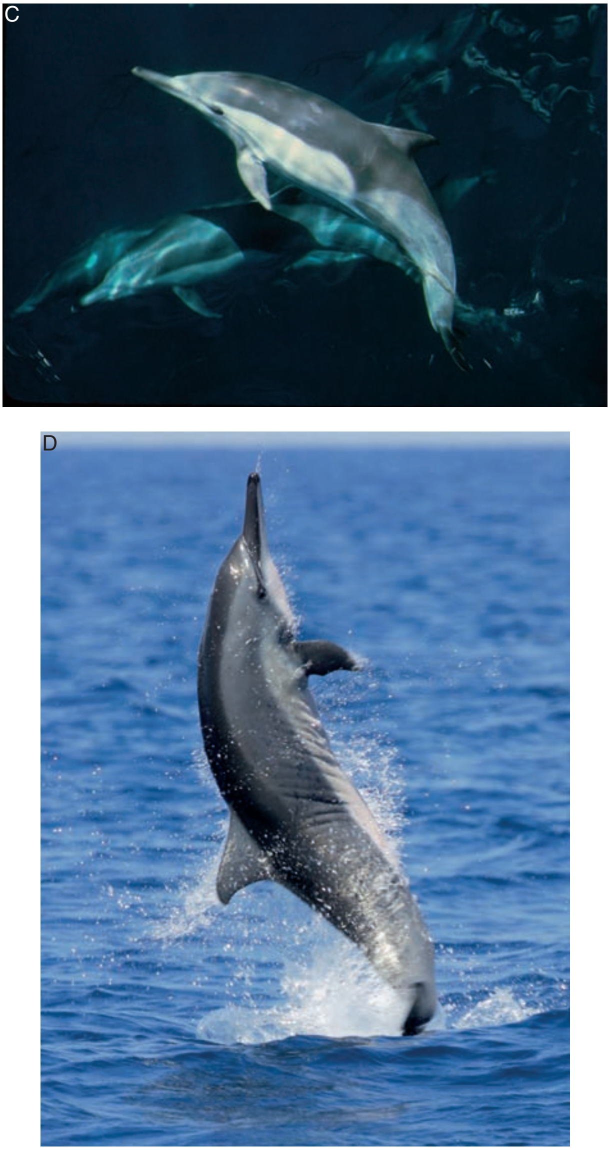


Figure 3.2 Examples of tropical and warm-water dolphins. (A) Short-finned pilot whale *Globicephala macrorhynchus*, (B) Atlantic spotted dolphin *Stenella frontalis*, (C) short-beaked common dolphin *Delphinus delphis*, and (D) spinner dolphin *Stenella longirostris*. Spotted dolphins develop their spots as they mature. Short-beaked common dolphins occur in nearshore and offshore waters of the Atlantic and Pacific oceans, while their long-beaked congenerics *Delphinus capensis* occur as well in the Indian Ocean, but always close to shore. (Photos courtesy of B. Würsig, L. Karczmarski.)

changes in water temperature and salinity; but they are protected from most storms. Coastal habitats describe open coastlines typically <100 m in depth and relatively close to shore (within several kilometres), lacking barrier islands, large protected bays or tidal marshes. Coastal habitats may be located just offshore of inshore areas, as found throughout most of the Gulf of Mexico, for example. These habitats are more exposed to storm systems, but often experience less dramatic seasonal variations in temperature and salinity. Neritic habitat describes the area over the continental shelf, which lies offshore of the coastal habitat. This area is typically <200 m in depth but does not include the surf zone or coastal waters. Dolphins in this habitat can be influenced by storm systems and some seasonal changes in temperature and salinity. Finally, the pelagic habitat represents deep-water areas over the continental slope and open ocean. This habitat shows less seasonal variation in temperature and salinity and has no barriers to movement. Dolphin communities can occupy more than one habitat, on daily, periodic, or seasonal basis and there can be overlap between categories.

The distribution of dolphin species can also vary between colder temperature to sub-polar and tropical waters. Typically, the more sub-polar species tend to have larger, thicker bodies than tropical dolphins, and this gradation can even be observed within species (e.g., bottlenose dolphins (*Tursiops* sp.; Wells and Scott, 1999). However, some rapidly moving small-bodied dolphins such as the hourglass dolphin (*Lagenorhynchus cruciger*) and Commerson's dolphin (*Cephalorhynchus commersonii*) and northern and southern right whale dolphins (*Lissodelphis* sp.) occur at high latitudes (Brownell and Donahue, 1999; Goodall, 1994).

2.2. Predation and predatory risk

Predation is an important factor that promotes sociality in many different species in a wide variety of habitats (e.g., Bertram, 1978; Jarman, 1974; Norris and Schilt, 1988). Individuals in groups may have a better chance of detecting predators, avoid being consumed, or cooperatively drive off predators (Bertram, 1978). In some cases, however, living in groups may actually increase predation risk to individuals if larger groups are more attractive or easily detected by predators (e.g., Hebblewhite and Pletscher, 2002). Therefore, group living may have both costs and benefits, and the net cost/benefit ratio depends on the specific predation conditions (Bertram, 1978).

In most locations where dolphins are found, only limited information is known about predation risk. Relatively few predatory attacks have been observed (see Connor and Heithaus, 1996; Gibson, 2006; Maldini, 2003; Mann and Barnett, 1999; Pitman *et al.*, 2003, for examples). Shark-inflicted scars on living dolphins can give some indication of predation risk, although these scars only represent non-lethal attacks. Approximately 74% of bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Australia bear shark-inflicted scars. Bottlenose dolphins in other area display lower scar rates (10–20% in South Africa, 31% in Sarasota, Florida, 37% in Moreton Bay, Australia) while dolphins in the open ocean and the Adriatic have few if any shark scars (Heithaus, 2001a). While it is clear that that many dolphins face predation by sharks and killer whales, the likelihood of predation and the strategies that dolphins use to avoid predation are very poorly studied. Although it is possible to draw some inferences about predation on dolphins, these remain for the most part, untested conjecture based on limited observations. Future studies will hopefully address and test predation questions more directly, similar to the scope of studies currently conducted in Shark Bay, Australia (e.g., Heithaus and Dill, 2002).

It is likely that predation is an important factor leading to the sociality of delphinids (e.g., Connor, 2000; Norris and Dohl, 1980; Norris and Schilt, 1988). Group living in dolphins likely reduces predation risk in several ways, although few studies have empirically examined delphinid group living and predation risk. First, by grouping, the distribution of dolphins becomes more heterogeneous in the environment. Thus, predation risk is lowered as a predator must search a larger area to locate prey (the encounter effect). However, aggregations of animals may be more easily detectable by predators, and this could actually increase the encounter probability (e.g., Bertram, 1978; Turner and Pitcher, 1986). Second, an individual dolphin's chance of being preyed upon is reduced within the group, as predators typically attack only one individual (the dilution effect; e.g., Childress and Lung, 2003; Foster and Treherne, 1981; Hebblewhite and Pletscher, 2002; Turner and Pitcher, 1986; Wisenden, 1999). Third and somewhat related to the dilution effect is the concept that individual dolphins may hide behind another individual (cover hypothesis; e.g., Bumann *et al.*, 1997; Hamilton, 1971). Under this hypothesis, different positions in the group have different associated risks, with the centre considered to be the safest (Bumann *et al.*, 1997). Fourth, being in a group can help in the detection of predators, as there are more individuals on the lookout (vigilance; e.g., Elgar, 1989; Pulliam, 1973). Additionally, dolphins in groups may cooperate by integrated communication to detect a predator (what Norris and Schilt, 1988, termed a part of the Sensory Integration System; see also Norris *et al.*, 1994), to confuse a predator or to cooperatively attack it (e.g., Bertram, 1978; Krakauer, 1995; Ostreiher, 2003).

Predatory attacks are often difficult to observe and may lead to difficulties in estimating predation risk, as has been confirmed in studies on primate predation (Stanford, 2002). It is especially difficult to estimate predation risk faced by dolphins, as many attacks will likely occur below the water surface and away from human observers. Major predators of dolphins include killer whales and sharks (Connor, 2000; Heithaus, 2001b; Jefferson *et al.*, 1991). However, as relatively few predatory attacks have been observed, little is known about how predation risk may vary between environments, species, group sizes and group composition.

Habitat characteristics may influence general predation risk. Complex habitats (such as enclosed bays, estuaries and tidal marshes) may provide elements behind which the dolphins can hide and thereby reduce their predation risk (e.g., Connor, 2000; Wells *et al.*, 1999a). Clear water may also help dolphins to detect predators (Heithaus, 2001b). The surf zone also represents an area where predators may have difficulty detecting dolphins (Heithaus, 2001b; Jefferson *et al.*, 1991), and near-shore dusky dolphins (*Lagenorhynchus obscurus*), for example, retreat to within the surf zone when killer whales approach (Würsig and Würsig, 1980). Spinner dolphins rest in clear shallow waters of island bays and lagoons, presumably to be able to scan their entire environment, and to reduce the possibility of attacks from depth (Fig. 3.3). They prefer to travel over expanses of sand, not variegated bottom as presented by coral beds, presumably due to the greater possibility of shark attacks in more complex substrata (Würsig *et al.*, 1994b).

Killer whales are found throughout much (but not all) of the world's oceans and they probably prey upon most species of dolphin, except those dolphins living far up river systems (e.g., Irrawaddy dolphin and tucuxi). Several species of dolphins are known to be killer whale prey, including long-finned pilot whales (*Globicephala melas*), common dolphins, dusky dolphins and spotted dolphins (*Stenella* sp. Connor, 2000; Jefferson *et al.*, 1991; Pitman *et al.*, 2003). Other species of dolphins, porpoises, mid-sized toothed whales and baleen whales also comprise the killer whale's prey (Jefferson *et al.*, 1991). There have been no documented predatory attacks

Figure 3.3 A resident group of spinner dolphins *Stenella longirostris* resting in shallow-water Midway Atoll lagoon, far-western Hawaii. (Photo courtesy of L. Karczmarski.)

on killer whales by other killer whales, although they have conspecific scars and toothrakes, these probably do not represent predation attempts. If killer whales do prey upon conspecifics, it appears to be extremely rare (Baird, 2000).

Killer whale population density varies greatly worldwide, and some dolphin populations are more at risk than others. Killer whales are most abundant in coastal waters in the higher latitudes, so offshore and tropical dolphins tend to face a lower predation risk from them (Dahlheim and Heyning, 1999). Some inshore areas may represent protected refuge from killer whales. The water may be too shallow for killer whales, or islands, bays, the surf zone, or kelp beds provide areas to hide (Fig. 3.4). Documented killer whale attacks on delphinids are relatively rare but indicate that groups of killer whales can effectively hunt seemingly healthy adult dolphins (e.g., Constantine *et al.*, 1998; Jefferson *et al.*, 1991; Pitman *et al.*, 2003).

Dolphins display a number of behavioural responses to the presence of killer whales. In many situations, dolphins and killer whales coexist in the same area, with no noticeable reaction of dolphins to killer whales. In fact in many of these situations, killer whales make no attempt to attack and prey species avoid fleeing from every potential attack (Jefferson *et al.*, 1991), and which is also commonly observed between terrestrial predators and ungulates (e.g., Caro *et al.*, 2004). In other situations, dolphins have been observed rapidly swimming away from the killer whales, forming tight groups with coordinated movements, rapid expansion of groups with animals swimming in many different directions, or hiding in shallow water or kelp beds (e.g., Constantine *et al.*, 1998; Jefferson *et al.*, 1991; Pitman *et al.*, 2003). It is likely that the motivational state of predator and prey will often determine the behavioural response of the prey (Lima and Bednekoff, 1999; Stankowich and Blumstein, 2005).

In some non-delphinid marine mammals, deep diving behaviour has been suggested to be an anti-predator strategy, with sperm whales

Figure 3.4 A group of Indo-Pacific bottlenose dolphins *Tursiops aduncus* in the surf zone off the southeast coast of South Africa. (Photo courtesy of L. Karczmarski.)

(*Physeter macrocephalus*) and elephant seals (*Mirounga* sp.) spending much of their lives deeper and for longer times than killer whales can dive. It is unlikely that this is an effective strategy for many dolphin species, as most dolphins appear to make similar depth dives as killer whales (Schreer and Kovacs, 1997 and references therein). In addition to killer whales, dolphins may also be preyed upon by false killer whales (*Pseudorca crassidens*) and pilot whales (Perryman and Foster, 1980); these predators probably represent less of a risk than killer whales worldwide, but may be important delphinid predators in tropical pelagic zones.

Most observations of shark predation come from coastal areas; however, this is also where the greatest research effort has occurred (Heithaus, 2001b). It should not be assumed that offshore areas have lower predation risk; in fact, predation risk may be highest in the open ocean where there is no place for dolphins to refuge (Wells *et al.*, 1999a). Indeed, the large dolphin groups found in the open ocean may be anti-predator responses (Norris and Dohl, 1980; Wells *et al.*, 1999a). Large-bodied sharks are capable of hunting adult dolphins, although the very large delphinids (e.g., killer and pilot whales) may only be vulnerable to shark predation as juveniles. Several different species of sharks are known to be important predators of delphinids, including great white (*Carcharodon carcharias*), bull (*Carcharhinus leucas*), dusky (*Carcharhinus obscurus*) and tiger sharks (*Galeocerdo cuvier*). Bull sharks range far up large rivers and prey upon riverine dolphins such as the tucuxi (Heithaus, 2001b). Several long-term studies of dolphins indicate that shark predation is an important source of mortality, and many individuals also bear the scars of shark attacks that have resulted in injury but not mortality (Heithaus, 2001b; Mann and Barnett, 1999; Wells *et al.*, 1987).

Several deep-water sharks are also likely predators of delphinids. The six-gill shark (*Hexanchus griseus*) is a large deep-water shark found along continental shelves and upper slopes. Off South Africa, it preys upon dolphins, and given its worldwide distribution is likely a major delphinid predator elsewhere as well (Heithaus, 2001b). Similarly, there is indirect evidence that broadnose seven-gill sharks (*Notorynchus cepedianus*) prey upon coastal dolphins, and these primitive sharks may be important predators in some southern hemisphere areas. Other species such as dusky and oceanic whitetip sharks (*Carcharhinus longimanus*) are probably occasional predators on delphinids. Little is known about the distribution and prey on most of the oceanic sharks, although short-fin mako (*Isurus oxyrinchus*), Pacific sleeper (*Somniosus pacificus*) and Greenland sleeper sharks (*Somniosus microcephalus*) are suspected dolphin predators, and further research will probably identify more shark species as dolphin predators (Heithaus, 2001b).

Levels of shark predation on delphinid communities vary between species and locations. In general, offshore cetaceans have fewer scars attributable to unsuccessful shark predation attempts than inshore cetaceans (Fig. 3.5 for an example of a shark bite scar). While this could indicate

Figure 3.5 Common bottlenose dolphin *Tursiops truncatus* in Tampa Bay, Florida, showing shark bite scars. (Photo courtesy of Eckerd College Dolphin Project).

lower predation risk in offshore waters, it also could indicate that inshore dolphins are more likely to survive a shark attack (Heithaus, 2001b). Some dolphin species appear more vulnerable to shark predation than others. Off the coast of KwaZulu-Natal, South Africa, humpback dolphins (*Sousa chinensis*) had higher scar rates than Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in the same area, perhaps suggesting greater predation pressure on the inshore humpback dolphins (Cockcroft, 1991). Predation rates may also vary by location with relatively high scar rates found on bottlenose dolphins (*Tursiops* sp., see Section 3.1 for brief discussion of *Tursiops* taxonomy) off Shark Bay, Australia, moderate scar rates off Moreton Bay, Australia and Sarasota, Florida, and very low rates in the Adriatic Sea (Heithaus, 2001a,b). Unsuccessful predation attempts can influence reproductive success. Injured female elephant seals rarely gave birth or engaged in mating behaviour, and therefore lost reproductive potential (Heithaus, 2001b). No similar evidence exists for the costs of unsuccessful shark attacks on delphinids, but they likely do occur (Heithaus, 2001b).

Dolphins also display a number of behavioural reactions to shark presence (reviewed in Heithaus, 2001b). Often, dolphins avoid areas where sharks are present (e.g., Corkeron *et al.*, 1987; Saayman and Tayler, 1979). When predatory sharks approach dolphin groups, strong flight responses can occur (e.g., Connor and Heithaus, 1996). In other situations, dolphin groups mob a shark and chase it out of the area (e.g., Heithaus, 2001b; Mann and Barnett, 1999; Saayman and Tayler, 1979). Predation is often cited as the major reason for the formation of dolphin groups (see Norris and Dohl, 1980; Wells *et al.*, 1980, 1987), but few data have been collected regarding this issue.

Finally, sharks and delphinid predators, such as killer, false killer and pilot whales, are likely to elicit at least some differences in dolphin prey detection and avoidance strategies. Sharks tend to strike independently and without warning, generally coming from depth and in this context can be viewed as essentially ambush predators. Killer whales and other predatory delphinids are social, and they chase down dolphins that are generally well aware of the predators' presence long before an individual is taken. While differences in detection and avoidance strategies have not been studied in detail, we expect that dolphins generally group tightly and use coordinated sensory awareness in the face of shark predation. To thwart predatory delphinid attacks, they are more likely to use strategies of hiding in surf zones or other areas of shoreline, and outmanoeuvre the generally larger social predator. Dolphins may also zigzag away in an attempt to confuse and disorient the mammalian predator.

It is likely that there is an overlap in the strategies to avoid each type of predator and that strategies will vary with differing habitats and predation pressures. For example, in South Africa, where killer whale predation is rare (although it occurs) but where shark predation is substantial, *T. aduncus* and *Sousa* sp. form tight groups and both species are seen just behind the breaking waves (Karczmarski, 1996; Karczmarski *et al.*, 2000a). Heaviside's dolphins (*Cephalorhynchus heavisidii*), when they are closer inshore in the early part of the day (Elwen *et al.*, 2006), also stay just behind the surf zone. In each of these cases, both strategies of tight grouping and hiding in the surf zone are most likely a defence against shark predation. This area of predator–prey interactions is ripe for study, as it may help explain differences in grouping strategies in different predatory environments.

Dolphins typically form dynamic groups, where group size and membership change frequently; this may represent individuals or subgroups altering their group size and structure relative to their activity state (e.g., foraging, resting and social; Gero *et al.*, 2005) and current habitat in relation to predation risk (Heithaus, 2001b; Wells *et al.*, 1999a). In Shark Bay, Australia, Indo-Pacific bottlenose dolphins were found in larger groups when foraging in shallow water (which also represented areas of higher predation risk) and when resting (a risky behaviour which typically occurred in deeper waters where shark densities were lower). When shark density was high, the dolphins foraged less in the risky but more productive shallow water (Heithaus and Dill, 2002). Age and sex differences were also noted in habitat use. Juvenile male dolphins foraged the most in the risky but productive shallow water, while females with dependent young avoided these areas. High-growth rates may be important for juvenile males to reach sexual maturity, and foraging in a risky habitat may be more profitable for them than for other age and sex classes (Heithaus and Dill, 2002). In Sarasota, Florida, male common bottlenose dolphins (*Tursiops truncatus*) that formed pairs were more likely to be found in the coastal Gulf of Mexico than solitary males. The Gulf of Mexico represents an area of high prey and predator density, likely indicating that the paired males were better able to safely forage in the riskier and more productive habitat than solitary males (Owen, 2003).

While studies on the relationships between dolphins and predators are currently being conducted, there are vast knowledge gaps about dolphin predators, their behaviours, predator distribution and dolphin responses. Dolphins likely face predation pressures in all habitats, with the possible exception of areas with very recent high shark fishing mortality (e.g., bottlenose dolphins in the Adriatic Sea; Bearzi *et al.*, 1997). Dolphins in varying habitats have apparently evolved ways to deal with predation; often these are behavioural responses, and in the open ocean there may be few options other than forming large groups. Competition for food or other factors may limit the option of forming large groups in coastal habitats. Further studies explicitly investigating these questions will aid our understanding of delphinid sociality.

2.3. Foraging behaviour and diet

While reducing predation risk clearly plays a role in the evolution of group living, individuals may also form groups in order to increase access to food resources (e.g., Beauchamp, 1998). Living in a group can increase access to food resources in several different ways at different times over the foraging cycle. By coordinating search effort, groups are often able to more readily locate large prey patches and minimize search time (e.g., Beauchamp *et al.*, 1997; Buckley, 1997; Ryer and Olla, 1995). Group living can also assist predators in capturing and handling large or difficult to catch prey (e.g., Blundell *et al.*, 2002; Creel and Creel, 1995). Grouping may also help individuals to defend a food resource against conspecifics, or individuals of other species (e.g., Boinski *et al.*, 2002; Gittleman, 1989).

Fish and squid represent the major prey species for most dolphins, although other prey types have been recorded. Diet is often correlated with body size, dentition and habitat. The largest of the delphinids, killer whales, false killer whales, pilot whales and Risso's dolphins (*Grampus griseus*), have relatively few large teeth and feed upon large fish or squid (Wells *et al.*, 1999a). Killer whales also prey upon other marine mammals, and false killer whales and pilot whales occasionally prey on smaller dolphins (see Section 5.1.2; Jefferson *et al.*, 1991; Perryman and Foster, 1980). The small pelagic dolphins (e.g., *Stenella* and *Delphinus*) typically have a high number of small interdigitating teeth in both upper and lower jaw. These teeth are well suited to capturing small schooling squid and fish. Swimming speed appears to be more important in these species, with a more streamlined body shape (Wells *et al.*, 1999a). Inshore and coastal delphinids (e.g., *Lagenorhynchus* and coastal forms of *Tursiops*) tend to have larger teeth that may assist in capturing larger prey. These species tend to be less streamlined and have larger flukes and fins than pelagic dolphins (Wells *et al.*, 1999a).

Dolphins have traditionally been considered to be rather opportunistic foragers, preying upon many different species. However, most of this work has been based upon identifying prey from stomach contents. More detailed work studying the foraging behaviour and diet of free-ranging dolphins has indicated that different communities have different prey preferences, which often reflect local prey distribution (Wells, 2003). For example, inshore bottlenose dolphins in Sarasota Bay, Florida, feed predominantly on pinfish (*Lagodon rhomboides*) and do not appear to eat cephalopods. In contrast, coastal bottlenose dolphins in the adjacent Gulf of Mexico waters commonly prey upon cephalopods (Barros and Wells, 1998). Prey preference differences can also vary seasonally, in response to both prey distribution changes and seasonal changes in metabolic needs (Wells *et al.*, 1999a). Lactating female dolphins often have different prey preferences, perhaps to maintain the increased metabolic demands of lactation, or to avoid leaving an unprotected calf at the surface while she forages at depth (Bernard and Hohn, 1989; Cockcroft and Ross, 1990; Wells *et al.*, 1999a). More refined data collection reveals strong individual differences, with individual dolphins showing specific preferences for prey type and foraging strategy, even within the same community (e.g., Mann and Sargeant, 2003; Nowacek, 2002; Sargeant *et al.*, 2007). Our understanding of delphinid foraging strategies will be enhanced with additional studies that focus on individual foraging behaviour.

Cooperative foraging has also been described or suggested in delphinids. Dolphins in the open ocean often swim in long parallel lines, up to several hundred metres wide. This may facilitate finding large and somewhat sparsely distributed schools of fish or squid (Würsig, 1986). Dusky dolphins off Argentina appear to cooperate to concentrate schools of Argentine anchovy (*Engraulis anchoita*). When a small group (6–15 individuals) of dusky dolphins locates a fish school, they swim around and under the fish school in an apparent attempt to tighten the prey and herd it towards the surface. If no other group of dolphins joins, the small group corrals prey for only several minutes, and may not actually feed. It is likely that a small group of dusky dolphins cannot both contain the prey ball and feed on it (a disruptive activity), and for successful feeding more dolphins need to recruit to the patch. If other groups join, group herding and feeding can continue for hours and involve up to 300 dolphins. Underwater observations indicate that dolphins are corralling the fish against the surface of the water, and that feeding does not begin until the fish are sufficiently contained. There is evidence that dolphins cooperate to feed and that larger group sizes are more efficient at foraging in this manner (Würsig and Würsig, 1980). Similar types of cooperative encirclement of schools of fish have been observed in long-beaked common (*Delphinus capensis*), Atlantic spotted

(*Stenella frontalis*), Frazer's (*Lagenodelphis hosei*) and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*; Wells *et al.*, 1999a; Würsig and Würsig, 1980). Other species probably also cooperatively locate and hunt prey, but descriptions are unclear. Killer whales that eat marine mammals clearly cooperate in hunting large prey and it is unlikely that a solitary killer whale could successfully kill a large baleen whale (Baird, 2000). When cooperatively foraging, dolphins often utilize large prey patches (e.g., a large school of fish, or large baleen whale) that contain sufficient resources for many individuals to share, and this likely reduces foraging competition.

Prey species in inshore and coastal areas may be found individually rather than in large schools. In these areas, dolphins have a greater tendency to forage individually with little to no cooperation (e.g., Nowacek, 2002). However, bottlenose dolphins in some areas forage by intentionally stranding themselves and their prey on muddy banks simultaneously and in a coordinated manner; however, they do so only in small groups (Hoese, 1971). Foraging behaviour may differ between locations, attributable to habitat differences. Humpback dolphins in Algoa Bay, South Africa, display little cooperation and forage individually over rocky reefs (Karczmarski and Cockcroft, 1999; Karczmarski *et al.*, 1997). In tidal channels of the Bazaruto Archipelago, Mozambique, they are seen in small cooperative groups that chase their prey against sand banks and sometimes intentionally strand (Peddemors and Thompson, 1994).

Inshore and coastal dolphins that feed predominantly on non-schooling fish probably experience competition with other group members for food resources. It is likely that dolphins most often experience scramble-type competition with no individual being able to exclude any other from the resource and all individuals share equally in the resource and its depletion. However, there have been a few observations that suggest contest-type competition may occur. Off Argentina, a smaller pod of killer whales (two individuals) was apparently displaced by a larger pod (seven individuals) several times at a pinniped rookery (Hoelzel, 1991). Similar displacement of a killer whale pod feeding on a school of herring (*Clupea harengus*) was also observed off Norway (Bisther and Vangraven, 1995). An apparent contest-type competition for favourable resting sites was observed in spinner dolphins associated with remote Midway Atoll, far-western Hawaii (Karczmarski *et al.*, 2005). Contest-type competition may also occur within groups. A dominance hierarchy appeared to form in bottlenose dolphins foraging near trawlers in Moreton Bay, Australia, with males receiving the most food (Corkeron *et al.*, 1990), although it was not clear in this study if females were avoiding the area nearest the trawlers because of increased risk of entanglement (Fig. 3.6). Few delphinid studies have specifically investigated the potential for scramble or contest-type competition between groups or group members; therefore, these few examples do not necessarily represent rare situations but instead examples of behaviour that is rarely examined.

Figure 3.6 **Common bottlenose dolphins *T. truncatus* travelling behind a shrimping vessel, surfacing here just above where the weighted net is touching the bottom. Dolphins feed directly in the net, as well as on fishes and invertebrates stirred up from the bottom by the net's passing. (Photo courtesy of T. Henningsen, with permission.)**

However, primate studies indicate the importance of both scramble-type and contest-type competition in the evolution of sociality (e.g., Isbell, 1991; Isbell and Young, 2002), and it would be valuable to conduct studies on delphinids to explicitly examine competition levels.

Pelagic prey species (typically fish and cephalopods) are typically found in rare but profitable patches, with large areas of habitat with little to no available food resources (Horwood and Cushing, 1978; Steele, 1985). Cooperative foraging to locate and corral this prey may help reduce competition levels, although little work has been done to investigate this issue. Interspecific displacement through contest-type competition may also occur. Many studies suggest that different species of dolphins segregate their habitats either temporally or spatially (e.g., Gowans and Whitehead, 1995; Griffin and Griffin, 2003; Hamazaki, 2002; Würsig and Würsig, 1980) and competitive exclusion may play a role.

2.4. Ranging patterns and daily movements

Delphinids display a wide range of patterns of daily and seasonal movements. Some dolphins, such as bottlenose dolphins in Sarasota, Florida, remain relatively resident year-round in a small home range, although some seasonal changes in distribution can occur (Owen *et al.*, 2002; Wells, 2003). In contrast, other dolphins appear to have seasonal migrations with long range movements (e.g., short-beaked common dolphins, *Delphinus delphis*; Goold, 1998, and Atlantic white-sided dolphins, *Lagenorhynchus acutus*; Reeves *et al.*, 1999), although relatively few studies have investigated individual movement patterns in these communities. However, all dolphins appear to have relatively high daily movements often exceeding 100 km d^{-1} (e.g., Mate *et al.*, 1994, 2005; Wells *et al.*, 1999b; Würsig and Würsig, 1980), in contrast to primates and terrestrial carnivores which rarely travelled more than 2 km d^{-1} (Wrangham *et al.*, 1993 and references therein). Delphinids routinely travel throughout the day, rarely resting, and can be exposed to large areas of habitat, or their entire home range on a daily basis, while primates and carnivores rest much more frequently, and do not cover as large an area on a daily basis.

Scramble-type competition can constrain group size, as in larger groups there are more individuals utilizing the same food resources. Because of difficulties in directly measuring levels of competition, indirect measures are often used. With increasing food density, scramble-type competition is predicted to decrease while group sizes increase. When travel costs between food patches are low, scramble-type competition is also predicted to decrease because it is energetically less expensive to find another food patch. In primates and carnivores, increased levels of scramble-type competition, measured by population density (an indirect measure of food density) and mean daily movements (an indirect measure of travel costs) are correlated with decreased group size. While the data do not discern whether increased group size drives increased mean daily travel or mean daily travel leads to increased group size, the hypothesis predicts that variation in daily travel drives the variation in group size (Wrangham *et al.*, 1993).

2.5. Socioecology

Socioecology investigates the evolution of social strategies in relation to environmental and ecological factors. Socioecological models that relate social structures to ecological parameters have been developed for several terrestrial taxa; however, models have not been developed in the same detail for marine animals. Thus we will present key concepts from these terrestrial models first, before looking at how marine models may be developed.

Primate socioecology has been investigated in the greatest detail, probably due in large part by a human desire to understand our own social behaviour. The general model relates female social strategies to availability of food and competition with conspecifics, while male social strategies are determined in large part by female distribution and bonding. When high-quality food resources occur in small defendable patches that only a discrete number of individuals can feed on at one time (e.g., a fruiting tree where there are only a few branches on which individuals can sit), contest-type competition occurs for access to the patches. When females can cooperate to exclude other females from the patch, the cooperating females benefit and long-term bonds and social groupings between females evolve (Wrangham, 1980). Males may be territorial, or defend a group of females. When food density is particularly high, a single male can defend a territory and the females within it. An extra male in the group would be unlikely to increase the defensibility of the territory, but would increase food competition within the group; therefore single male groups form. When food density is lower, home ranges become too large to be defended as a territory and males guard female groups. In these situations, cooperation between males is beneficial in competitive interactions with neighbouring groups, and multi-male groups occur (Wrangham, 1980). When long-term bonds form between females, subadult males are often forced to leave their natal group, and reproductive skew among males is high (see Koenig, 2002, for a recent review of primate socioecology models).

Ungulate socioecology has also been well studied following a seminal paper by Jarman (1974) that related African antelope social organization to their feeding style, ranging behaviour and anti-predator behaviour. Food availability and dispersion varies greatly between feeding styles and some species may range widely, undergoing annual migrations to remain in areas of optimal growth. Small groups of small antelope feed more selectively than large groups of large bodied antelope. Similarly, smaller groups of antelope tend to remain inconspicuous from predators, while larger groups flee (see Brashares *et al.*, 2000, for a recent review).

Most carnivores tend to be relatively asocial; grouping only during the breeding season, but some species live in social groups year round (Gittleman, 1989). Territory acquisition appears to drive the evolution of group living in carnivores, such that animals may group to exploit a high-quality territory that can support them during periods of low resource availability (see Bekoff, 2001; Clutton-Brock, 2002; Johnson *et al.*, 2002, for a review of different theories). Once in groups, individuals can benefit from anti-predatory strategies or cooperative exploitation of resources. Typically, the smaller carnivores receive greater anti-predator benefits than the larger carnivores, although many small carnivores are solitary (Gittleman, 1989). For some larger-bodied carnivores, infanticide may be the main form of predation, promoting the grouping of related females and male–female bonds outside the breeding season (e.g., lions, *Panthera leo*; Packer *et al.*, 1990). Competition for food resources may influence group sizes and sociality. With low food availability, carnivores typically have small litters and may be solitary or live in small groups. However, when food is abundant, large groups form with larger litters (Geffen *et al.*, 1996; Wrangham *et al.*, 1993). For most group living carnivores, grouping increases foraging success and in particular, cooperative hunting may widen the available prey base as groups of animals can successfully hunt larger animals than solitary individuals (Gittleman, 1989). The benefits of cooperative hunting in carnivores has been controversial, with some studies reporting little benefit (e.g., lions; Packer and Caro, 1997; Packer *et al.*, 1990, but see Stander, 1992) while others argue that sociality is driven by the energetic benefits of communal hunting (Creel, 1997, 2001; Creel and Creel, 1995); however, it is clear that some species engage in cooperative hunting.

2.5.1. Delphinid socioecology

It is perhaps useful to think of delphinids as having the social intelligence/thought processing capabilities of primates, the foraging requirements of carnivores and the predation pressures of ungulates. Given this, we believe there is much to be gained by incorporating aspects of models based on other taxa and relating these specifically to delphinids. A conceptual framework may assist in the understanding of delphinid group size and social structure. In particular we focus on the role that the spatial and temporal predictability of resources plays in the determination of ranging patterns of individuals and communities. As movement from one area to another may be energetically expensive or expose an individual to predation risk, individuals will likely minimize movements to range only as widely as needed to find sufficient resources. In many situations, the availability of food resources will be the most critical factor, although other resources such as habitat safe from predation, mating partners and appropriate thermal habitat may also be important. Females, in particular, are likely to minimize their movements, as they attempt to ensure the survival of each offspring. The observed range of movements of individuals then influences social strategies, including anti-predator and foraging behaviour as well as levels of competition between individuals.

We propose a socioecological model that predicts when resources are spatially and temporally predictable, dolphins will remain resident in relatively small areas. However, in these smaller areas, scramble-type competition may increase and thus we predict that group sizes should become smaller. In contrast, we predict that when resources are spatially and temporally variable, dolphins cannot remain resident but must instead range widely to find sufficient resources. This increase in ranging behaviour is predicted to be correlated with increased group size. In larger groups, scramble-type competition can be reduced by cooperative foraging to more effectively find and exploit large prey schools (Fig. 3.7). Additionally, larger groups provide anti-predator benefits to group members. Thus variable resources will lead to the formation of large groups of dolphins which range over large spatial scales. In contrast, predictable resources will lead to the formation of small resident groupings of dolphins. We will investigate this model by comparing observations of delphinid social strategies in different habitats. None of these studies were designed to empirically test these hypotheses; however, they can yield some important insights into the evolution of delphinid sociality.

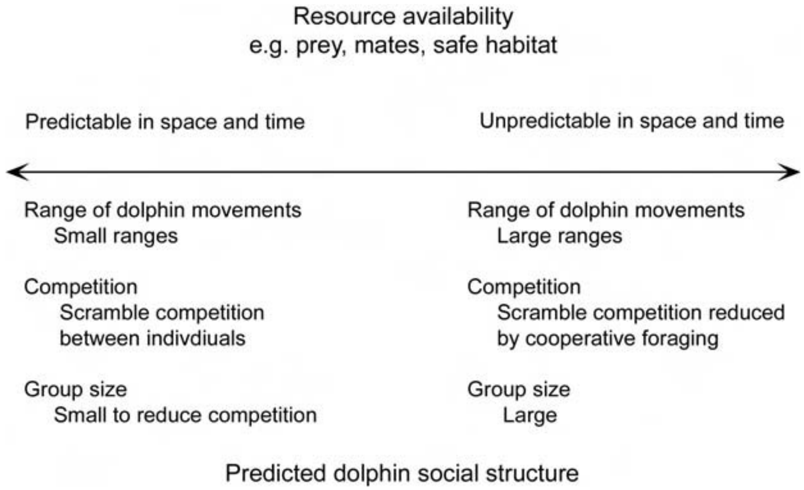


Figure 3.7 Socioecological model of the influence of the predictability of resources on ranging behaviour, scramble-type competition levels and group size.

This framework builds on an earlier descriptive model by Wells *et al.* (1980, 1999a) which emphasized ecology and anti-predator strategies as important factors driving the social structure. In coastal and offshore waters, habitat structure is relatively simple, leaving few areas to hide from predators. In these areas, group formation provides the only effective anti-predator strategy and thus large groups are favoured. However in inshore waters, with barrier islands, tidal marshes and shallow areas, dolphins are able to refuge from predators and therefore there is less selection pressure to form large groups to avoid predation (Wells *et al.*, 1999a). Anti-predatory strategies are clearly an important component selecting for group living in delphinids; resource predictability and competition levels, however, are at least equally important. The conceptual framework proposed in this chapter explicitly includes both resource acquisition and anti-predator strategies. Additionally, this framework is built upon predictions about delphinid social strategy that can be tested in the future.

Some delphinid communities can be categorized into either the resident or wide-ranging pattern. Several well-studied communities of bottlenose dolphins (e.g., Shark Bay, Australia and Sarasota Bay, Florida; Connor *et al.*, 2000b) clearly fit the resident pattern, while many of the offshore communities (e.g., spinner, spotted and bottlenose dolphins in the Eastern Tropical Pacific; Johnson and Norris, 1994; Pryor and Kang Shallenberger, 1991; Scott and Chivers, 1990) fit the wide-ranging pattern. However, there are other communities that are not easily described by this simple dichotomy. Their ranging pattern and social structure appears to be an intermediate form between the two extremes, and we believe that delphinid ranging behaviour and social structure forms a continuum, with most communities considered within the context of resident, wide-ranging or intermediate (Fig. 3.7). Currently, the discussion of these community descriptions can only be conducted in a relatively superficial, qualitative manner as few communities have been studied in sufficient detail for more than generalities. However, we anticipate that the proposed framework may provide a starting point to examine the evolution of social strategies in delphinids in more detail. We also hope that quantitative analyses of this and more refined frameworks can be conducted in the future, similar to recent quantitative tests conducted by Brashares *et al.* (2000) on Jarman's original model for describing African antelope sociality (Jarman, 1974).

3. RESIDENT COMMUNITIES

The model we proposed suggests that when resources are predictable in space and time, individuals remain resident in a relatively small area (Fig. 3.8). Long-term residency leads to individuals having intimate knowledge of their habitat, and therefore knowledge about where food resources and predators are most likely to be found. Thus, individuals may be able to reduce predation risk by avoiding high risk areas. Many of the areas with predictable resources are inshore areas with estuaries and marshes; in these areas the habitat is suitably complex for individuals to hide from predatory attack. Hence, in many of these resident communities there may be less advantage in grouping as an anti-predator strategy and group sizes may be smaller. Within a small resident area, a smaller quantity of food is likely to be available, which supports a smaller community of individuals. In many of these areas, prey tend to be found individually or in small schools, so there is an advantage to foraging alone or in small groups to reduce competition with little to no advantage to cooperative foraging. Predation risk and resource availability then lead to small communities of individuals composed of small groups. It is also true that in many inshore areas, there is simply not enough physical space for a large group of animals to exist, similar to the restriction of space faced by forest antelopes as opposed to open savannah antelopes.

The proposed model predicts that within these small resident communities, there will be little advantage to a female to be in a group as she can reduce foraging competition by being solitary. However, when a female has a dependent calf, predation risk increases dramatically and females often form nursery groups to reduce predation. In this situation, females may form loose associations with each other, and may preferentially associate with other females in similar reproductive state. As females tend to not form strong bonds with each other, it may be possible for males to sequester a

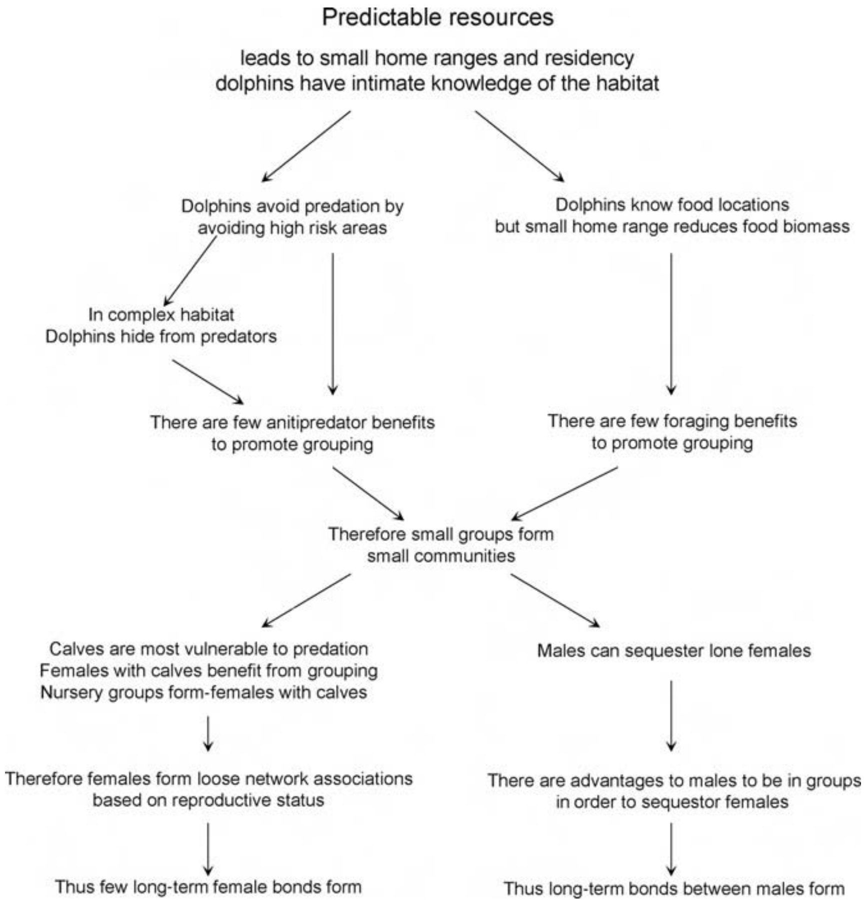


Figure 3.8 Model conceptual framework describing the influence of predictable resources on delphinid social strategies. There are few benefits to forming large groups in resident dolphins, either as a way to reduce predation risk or to increase access to food. Thus, communities of resident dolphins are relatively small and composed of small groups. It is unlikely females will form long-term bonds, although males may form long-term bonds in order to sequester females.

female for an entire oestrus cycle. This leads to competition between males to gain access to females (Fig. 3.9). In these situations, male–male cooperation may be helpful to guard females from other males as is often seen in chimpanzees (*Pan troglodytes*; Watts, 1998 and lions; Packer and Pusey, 1982). This is likely to lead to the development of strong bonds between males. In this scenario, maternal kin bonds are most probably known within the community as adult individuals are likely to associate at least on occasions with their mothers and her dependent offspring.

Figure 3.9 Common bottlenose dolphins *T. truncatus* near shore at Isla del Coco, Costa Rica. Male bottlenose dolphins (as shown here) often mouth and rake each other with their teeth, as displays of dominance or social play. (Photo courtesy of B. Würsig.)

3.1. Inshore bottlenose dolphins (*Tursiops* sp.)

Bottlenose dolphins occur in warm temperate to tropical waters, very close to shore, in bays and even mouths of rivers as well as in the open ocean. They are almost cosmopolitan in distribution, perhaps the most widespread delphinid alongside the killer whale (Wells and Scott, 1999). Bottlenose dolphins occur in different forms from about 2–3.8 m in size and from very light to almost black with a countershaded body colouration. They are not disruptively coloured, which suggests that their countershading allows for stealth in both approaching prey and avoiding predators. Smaller animals tend to live in warmer waters, and large animals occur in colder waters and further offshore, at least in the southeastern United States. Because of their almost continuous distribution along shores in many parts of the world, it is no surprise that there are apparent clinal morphological and genetical differences, as well as differences between inshore and offshore forms (Hersh and Duffield, 1990; Leduc *et al.*, 1999; Wells *et al.*, 1987).

The taxonomy of bottlenose dolphins is unsettled, but it is presently recognized that there are at least two forms sufficiently different to deserve species status, the common bottlenose dolphin (*T. truncatus*) that occurs throughout most tropical to warm temperate parts of the major oceans; and the Indo-Pacific bottlenose dolphin (*T. aduncus*), that occurs from the eastern coast of Africa, into the Red Sea and Persian Gulf, and to the western Pacific Ocean as far north and east as Taiwan (Ross and Cockcroft, 1990; Wang *et al.*, 1999). Some evidence suggests that the South African population should be considered a possible third species, but it has not yet been recognized (Natoli *et al.*, 2004). At present, it is believed that *T. aduncus* is largely if not exclusively coastal. It has a longer rostrum than that of *T. truncatus*, and tends to develop ventral spotting as it becomes sexually mature (Natoli *et al.*, 2004; Ross and Cockcroft, 1990; Wells and Scott, 2002).

There have been numerous behavioural/social organization studies of bottlenose dolphins worldwide, since early work that described a general fission–fusion society within communities close to shore (Argentina: Würsig, 1978; Würsig and Würsig, 1977; Florida: Wells *et al.*, 1987; Texas: Shane, 1980). The fission–fusion nature of dolphin societies has been compared superficially to societies of chimpanzees and spider monkeys (*Ateles geoffroyi*; originally by Würsig, 1978, and see Connor *et al.*, 2000b; Wells and Scott, 1999, for an update), but with the details of comparisons lacking until quite recently. The most detailed descriptions of bottlenose dolphin societies have come from two areas; for *T. truncatus* since 1970 in Sarasota Bay, Florida, and for *T. aduncus* since 1982 in Shark Bay, Western Australia (summarized in Connor *et al.*, 2000b; Wells and Scott, 1999). We present social strategy synopses of these two study areas, with comparisons from other studies as well. We recognize that differences in society structure described below might be due to phylogenetic differences, or an expression of environmental pressures. However, as the taxonomic classification only recently separated *T. truncatus* from *T. aduncus*, we present information for both in the following paragraphs, and we hope that future research will clarify whether the social evolution of these species should be considered separately.

Most of the well-studied bottlenose dolphin populations are composed of relatively small communities which remain resident in a small area over very long times. In Sarasota Bay, Florida, approximately 100 individual dolphins reside in an area about 125 km^2 and these dolphins and their offspring have been documented to have used this area for almost 30 years (Wells, 2003; Wells *et al.*, 1999a). This community's home range consists of shallow estuarine bays and channels behind a row of barrier islands that separate it from the Gulf of Mexico. There are several deeper passages to the Gulf of Mexico and the dolphins occasionally venture into the more open waters on the gulf side of the barrier islands (Owen *et al.*, 2002). Similar-sized communities of bottlenose dolphins with similar home ranges have been studied in protected areas near Galveston, Texas (community size = 28–34 individuals; home range = about 100 km^2; Irwin and Würsig, 2004), Moray Firth, Scotland (community size = 130; home range = under 100 km^2; Wilson *et al.*, 1997, 1999), Moreton Bay, Australia (community size = 250; home range = 350 km^2; Chilvers and Corkeron, 2001), and Fjordland, New Zealand (community size = 65; home range = 85 km^2; Lusseau *et al.*, 2003). In these areas, groups are typically composed of a small number of individuals (mean group sizes range from 3 to 10 individuals; Connor *et al.*, 2000b, and references therein). However, most of these communities are not isolated or closed. Instead other communities of bottlenose dolphins occur in adjacent habitats, and non-resident individuals are often observed within one community's core range area.

Predation risk is ever present for most bottlenose dolphins, and shark predation has been well documented in Shark Bay, Sarasota, South Africa, and elsewhere (Connor *et al.*, 2000b). Interestingly, in the Moray Firth of Scotland and in Fjordland, New Zealand, two areas of occurrence at the very extremes of bottlenose dolphin ranges, the occurrence of sharks and other predators appear to be very rare or non-existent. In Moray Firth, dolphins habitually show strong aggression towards harbour porpoises (*Phocoena phocoena*; Patterson *et al.*, 1998), and may limit harbour porpoise occurrence in the area by their aggression. It is unknown whether the absence of predation risk allows them the flexibility (i.e., time and energy) to show such strong aggression towards another species.

During the summer months when tiger sharks are present in Shark Bay, Australia, dolphins occur in larger groups over shallow waters where sharks are more common. Mothers with calves avoid shallow waters when sharks are present, while juvenile males commonly enter these areas of rich food resources (Heithaus and Dill, 2002; Mann and Watson-Capps, 2005). Similarly, paired male dolphins off Sarasota, Florida, are more commonly observed in coastal gulf waters, which are more productive, and these paired males have higher shark predation risk than do solitary males (Owen *et al.*, 2002). Such observations indicate that dolphins in both communities have intimate knowledge of their core habitat and alter their behaviour and distribution in relation to predation risk and prey densities.

Bottlenose dolphins have diverse food aggregating and capturing techniques from feeding singly to highly coordinated groups. During solitary foraging, they tend to feed on solitary, bottom- or rock-dwelling nearshore prey; when feeding in coordinated fashion, it is often on schooling fishes (Würsig, 1986). Bottlenose dolphins feed in association with shrimp and other trawling activities worldwide, having learned to take advantage of debilitated by-catch (Corkeron *et al.*, 1990), as well as to take fishes and other prey directly from nets (Cox *et al.*, 2003). They even feed in association with humans, when dolphins drive prey towards fishers' nets near shore, and both dolphins and humans appear to benefit from the coordinated manner of interspecies activity (Pryor *et al.*, 1990). In Shark Bay, some dolphins wear sponges on their rostra, as an apparent tool to poke at prey in crevices (Smolker *et al.*, 1997); in the Bahamas, dolphins detect prey under the sand, with their echolocation, and then 'corkscrew' into the substrate to obtain the prey (Rossbach and Herzing, 1997); and in small estuaries and marshes of the southeastern United States, dolphins coordinate lunges to chase prey onto sand banks, where fish can be snapped up while they are out of the water. The latter example is one of especially pertinent societal learning, cooperation, role playing and potential reciprocity, but details of interactions of known and potentially related individuals have not yet been described (Petricig, 1995). Community level differences in foraging strategies appear to be common among bottlenose dolphins and are likely linked to prey differences between areas (Mann and Sargeant, 2003; Sargeant *et al.,* 2007). However, strong individual differences in foraging strategies have been documented in Sarasota, Florida (Nowacek, 2002) and Shark Bay, Australia (Mann and Sargeant, 2003; Sargeant *et al.*, 2007), and these strategies may be passed from mother to offspring.

There is some evidence that bottlenose dolphins occur in smaller groups when feeding on lone or scattered prey, and in larger aggregations when feeding on schooling prey (often in deeper water and further from shore), but these assertions have not been definitively tested (Acevedo-Gutierrez, 2002; Acevedo-Gutierrez and Parker, 2000; Würsig, 1978). The general relationship is probably highly variable. Since larger groups tend to occur in somewhat deeper offshore waters, the relationship to foraging on schooling prey is confounded by a potential need to be in larger groups due to deep-water shark predation. Bearzi *et al.* (1997) noted that bottlenose dolphins of the Adriatic Sea east of Italy do not occur in larger groups in offshore waters, where there is very little to no shark predation as to sharks having been overfished in that area of the Mediterranean. On the other hand, in Shark Bay, Australia, shark predation is higher in coastal than offshore waters, and dolphins occur in variably sized but generally small groups offshore (Heithaus and Dill, 2002).

Many but not all females in Shark Bay and Sarasota occur in bands with close associations, of several to about 13 individuals, although there is fluctuation of band membership from day to day. This is because females have a larger network of other females (and males) with whom they associate with less frequency than with band members. Some females occur solitarily more often than they are associated with others, and there is some evidence that lone female or females and their most recent calves are more vulnerable to shark predation than those occurring in bands or mixed groups (Connor *et al.*, 2000b).

In Shark Bay, males form alliances that last from days/weeks to several years (up to 17 years, Connor *et al.*, 1992; Krützen *et al.*, 2004). First-order alliances consist of long-term stable associations of generally two to three males. These small alliances tend to be of related males, and they often sequester or coerce certain maturing or adult females to stay with them, and repeatedly copulate with them. Second-order alliances consist of several of these first-order ones, to take females from other alliances or to protect themselves from other male alliance raiders. These also tend to consist of animals related to a higher degree than expected by chance. Highly labile short-term 'super alliances' consist of one dozen or so males that raid other alliances of females, but that, interestingly, do not have greater-than-chance-expected relationships. Super alliances are short term, and perhaps may be thought of as 'gangs' that coalesce to intimidate and mate with females that might otherwise not be available to only one of the individuals (Krützen *et al.*, 2003). Alliance formation, presently described in detail only for Shark Bay bottlenose dolphins (but known or suspected in several other dolphin systems; see below), appears to have at least superficial parallels in chimpanzee (de Waal, 1982; Nishida and Hosaka, 1996; Watts, 1998), spider monkey (Chapman, 1990; Chapman *et al.*, 1995) and lion (Packer and Pusey, 1982) male alliances.

Adult males in Sarasota are more often solitary (or in long-term closely bonded pairs) than in Shark Bay, and more often in mixed-sex associations with females and youngsters of variable ages. While there are often long-term pair bonds of unrelated males (Owen *et al.*, 2002; Wells, 1991), there may be no or few strong male alliances and there is less evidence of males coercing unwilling females than in Shark Bay (Wells and Scott, 1999). It is also possible that the tendency for more often being alone or in small groups in Sarasota is due at least in part to a presumed lowered risk of predation by sharks in Sarasota than in Shark Bay. The detailed descriptions of alliances in Shark Bay (e.g., Connor *et al.*, 2000b) may somewhat overshadow the fact that males in Shark Bay are also found in association with mixed sex and age groupings and that not all mating strategy by males rely on the formation of alliances to sequester and coerce (at least at times) unwilling females. Alliance formation is only one of several mating strategies, as males with a variety of different association patterns successfully sire offspring (Krützen *et al.*, 2004), and there may be much more female choice and courtship behaviour than has been described to date.

Male alliances have also been documented in Port Stephens, Australia (Möller *et al.*, 2001), and off the Bahamas (Parsons *et al.*, 2003), but not in the Moray Firth, Scotland (Wilson, 1995). Formation of male alliances may be correlated with population density, as areas with high densities of dolphins lead to increased competition between males for access to females, and thus the only viable strategy for weaker males may be to form alliances for a chance at reproductive success (Connor *et al.*, 2000b). Observed population densities of bottlenose dolphins support this hypothesis: in Shark Bay, all or almost all males are found in some type of alliance and it has the highest density of dolphins; while in Moray Firth, there is no evidence for alliances, and density is low (Connor *et al.*, 2000b). Recently, modelling studies have been used to explore prevalence and group sizes of alliances relative to rates of encounter of males and females, aspects of resource utilization and presumed costs of switching alliances. These models await detailed testing in nature, but appear particularly applicable to strongly fission–fusion societies, as are most delphinids (Connor and Whitehead, 2005; Whitehead and Connor, 2005).

While all bottlenose dolphin societies studied to date show a varying nature of affiliations and fluid group structure, this tendency is least strong in a community of dolphins in Doubtful Sound, western coast of the South

Island, New Zealand (Lusseau *et al.*, 2003). There, dolphins occur in a mean school size of 17.2 individuals, appreciably larger than the generally <10 animals found in other areas, even after different definitions of 'school' or 'group' are taken into account. In Doubtful Sound, dolphins live in large mixed-sex schools, with strong associations within and between sexes, instead of the male alliances, lone males or lone females, and female bands that are more common in Shark Bay and Sarasota. Many associations are long lasting, with no permanent emigration or immigration into the community noted in seven years of study. The community structure is thus relatively stable, and constant companionship is the most prevalent pattern of association; however, group membership is still fluid, and groups fission and fuse. Lusseau *et al.* (2003) hypothesize that this unprecedented (for bottlenose dolphin societies studied to date) stability may be related to the isolation of Doubtful Sound from other sounds and bays amenable to dolphin habitation, and perhaps the low food productivity of the sound system. Low interaction with others may be simply due to distance to other communities, keeping the community of 100 or so dolphins in Doubtful Sound relatively closed, and tighter associations form between those animals that are present (Lusseau *et al.*, 2003). Additionally, food requirements may dictate that the dolphins spend more time foraging than time and energy spent on sexual pursuits, alliance-related strategies and 'politics' of association (*sensu* de Waal, 1982; for chimpanzees) than they do in the more food-rich areas of Shark Bay, Sarasota, and several other bottlenose dolphin habitats/locations. The interesting closed nature of the Doubtful Sound community shows several similarities with what was recently discovered for atoll-living spinner dolphins (Karczmarski *et al.*, 2005 and Section 3.2).

In summary, bottlenose dolphins of Sarasota Bay live in rather small and open society groups that travel little, probably due to the protected nature of the inshore environment and with reliable food resources year-round. The food resources are not so abundant, however, that they would support larger schools of dolphins, as often seen in the open ocean. Perhaps we might think of this as generally a scramble-type competition society. Females and young travel little, and stay in the most protected bays, away from storms and predators. Young and adult males travel more widely, and it is assumed that adult males are in search of oestrus females in different areas and communities. Bottlenose dolphins of Shark Bay have a somewhat similar social system, except that males form alliances to sequester females. Males may stay together in large part due to danger from sharks, and these associations allow them to then overwhelm and 'kidnap' certain females near or in oestrus. In the more isolated, predator-free and food-poor area of Doubtful Sound, New Zealand, bottlenose dolphins form the most closed mixed-sex society found in this genus to date. In general these observations fit well with our predicted model (Fig. 3.8) forming relatively small resident groups. The studies conducted in Sarasota and Shark Bay represent the longest, most comprehensive studies of delphinid sociality and ecology. However, there are still many gaps in our understanding of these dolphins. Continued research on individual differences in foraging behaviour and competition levels as well as predation risk will provide valuable tests of this framework. Conducting similar long-term comprehensive studies investigating bottlenose dolphin sociality, foraging behaviour and predation risk in other habitats will also further our understanding. The differences observed between these communities of bottlenose dolphins may relate to differences in predation pressure and resource predictability. Definitive tests of this model await detailed measurements of predation levels and resource availability.

3.2. Spinner dolphins (*Stenella longirostris*)

The spinner dolphin is a pantropical species, inhabiting tropical, subtropical and some warm temperate waters in the Atlantic, Pacific and Indian oceans. They are found from coastal to pelagic waters, but rarely they are located far from deep-water access. Similar to most other members of the genus *Stenella*, spinner dolphins are thin-bodied and streamlined, with a long and thin rostrum, short flippers and small tail. They are countershaded light below and dark above, with paintbrush stripes along their flanks (Perrin, 1998; see Fig. 3.2).

Several subspecies are recognized (Perrin, 1998). The Gray's (or long-beaked) spinner dolphin (*S. longirostris longirostris*) associates with tropical island systems and represents a 'semi-pelagic' form. Two other subspecies, the Central American (*S. longirostris centroamericana*) and eastern spinner (*S. longirostris orientalis*), are known from the Pacific coast of meso-America and pelagic Eastern Tropical Pacific, respectively (Perrin, 1998). Another pelagic form, an apparent hybrid between *S. longirostris orientalis* and *S. longirostris longirostris*, the so-called 'white-belly spinner dolphin' occurs throughout most of the offshore Eastern Tropical Pacific (Perrin, 1998; Perrin and Gilpatrick, 1994). Another subspecies, the dwarf spinner dolphin (*S. longirostris roseiventris*), occurs in shallow coastal waters of Southeast Asia from Malaysia to northern Australia (Perrin and Gilpatrick, 1994). The degree of sexual dimorphism varies among the subspecies, with males in general slightly larger than females, with the mean total length of most populations around 220 cm for adults. In the eastern Pacific forms, adult males develop a prominent post-anal keel and erect dorsal fin. In the white-belly form, this sexual dimorphism is present but muted, and in the Gray's form, it is even less pronounced, but still distinguishable. Spinner dolphin behavioural ecology has been studied off the west coast (known also as the Kona coast) of the Big Island of Hawaii (Norris and Dohl, 1980; Norris *et al.*, 1994; Östman, 1994), off the island of O'ahu, Hawaii (Lammers, 2003), off Moorea in French Polynesia (Poole, 1995), and most recently, in remote atolls such as Kure and Midway Atolls at the far-western end of the Hawaiian Island chain (Karczmarski *et al.*, 2005). In all cases, the Gray's spinner dolphin was studied, a subspecies that in Hawaii is often nicknamed 'Hawaiian spinner dolphin' (hereafter referred to as 'spinner dolphin'). Population figures are known in some detail only for the remote atoll communities, 120 and 260 dolphins at Kure and Midway Atoll, respectively (Karczmarski *et al.*, 2005), with each atoll approximately 10 km in diameter. For the Big Island's Kona coast, a population of at least 2000 dolphins (possibly more) has been suggested (Würsig *et al.*, 1994a), but a functional community size and home ranges remain unknown.

In pelagic waters as well as near islands and atolls, spinner dolphins feed at night on small mesopelagic fishes and squid that rise with the deep scattering layer towards the ocean surface at night (Perrin and Gilpatrick, 1994); but at least one form, the dwarf spinner dolphin, feeds on benthic fishes and invertebrates in generally shallow seas (Perrin *et al.*, 1999).

The pelagic and semi-pelagic spinner dolphins probably face high shark predation pressure, especially while feeding on the deep-scattering layer, although this has not been clearly documented (Heithaus, 2001b). In all areas studied, the semi-pelagic spinner dolphins use the inshore island habitat (or atoll lagoons) for daytime rest and social interactions. It is probable that sheltering in shallow water while resting during daytime reduces predation risk, and that the interaction between feeding in deep waters at night and resting close to shore in day drives much of the observed social structure of spinner dolphins in Hawaii (Norris and Dohl, 1980; Würsig *et al.*, 1994b).

Off the Big Island of Hawaii, Gray's spinner dolphins have a marked fission–fusion system, with smaller groups of <100 individuals close to shore during daytime, larger ones of several hundred (apparently aggregations of daytime groups) offshore at night, and then again in smaller aggregations near shore on the next day. Group composition changes from day to day, with some animals present on subsequent days, but others having 'switched to' other groups in other areas, generally in adjacent or nearby bays. Much of the earlier research was conducted in and near the Kealake'akua Bay of the Kona coast; a shallow bay 2km wide by 1km long. In this bay, mean group size was about 35 dolphins. The animals entered the bay 0.5–2.0 h after sunrise, socialized and rested in the bay most of the day, and left the bay with much social activity and leaping 1–3 h before sunset. Thus, dolphins stayed in the bay longer in summer than winter, and evidence from radio tracking (Würsig *et al.*, 1994b) and stomach content analyses (Norris and Dohl, 1980) indicates that dolphins travel to deeper waters in the evening to feed on prey associated with the nighttime rising deep-scattering layer. This supposition has recently been refined, with information to indicate that while in a large aggregated school at night, dolphins tend to forage in coordinated pairs at depth (Benoit-Bird, 2004; Benoit-Bird and Au, 2003).

It has been suggested that spinner dolphin day–night behaviour and group fission–fusion are related to efficiency of detecting and thereby avoiding shark predation in deep water while concentrating on feeding at night, and refuging from predators during social–sexual activities and resting during daytime. In this scenario, it is best for dolphins to aggregate for nighttime foraging, as more dolphins indicate greater chances of detecting deep water sharks (Norris and Dohl, 1980; Norris *et al.*, 1994; see Section 2.2 for predation theory). At the same time, bays provide excellent refuges during the day, but bays only allow efficient use by a certain number of dolphins, thus the fission–fusion system. Indeed, smaller bays than Kealake'akua Bay tended to have smaller daytime resting schools, providing some support for this idea. The situation may be somewhat similar to that of dusky dolphins off the Kaikoura Canyon, New Zealand, that also feed on deep-scattering layer-associated prey at night and rest near shore during the day (Benoit-Bird *et al.*, 2004, see Section 4.3 for more details).

For spinner dolphins found off the coasts of the Big Island of Hawaii, changes in affiliations of individual dolphins and bays used from day to day may indicate that dolphins consider each other as part of the larger group or community off a particular area, such as the Kona coast of the Big Island, and that they do not need constant close affiliation with certain members of that community. Although there might be some more tight bonds at the intra-group level, beyond the obvious mother–calf bonds (and certain pairs and trios of males, as suggested by Johnson and Norris, 1994; Östman, 1994), data gathered so far indicate a fluid society with dynamic groups of constantly changing membership; naturally leading to easy changes in group or school size from day to day.

Mating strategies of the Kona coast spinner dolphins remain little known. Anecdotal observations and the muted sexual dimorphism indicate that the basic system is one of multi-mate (polygynandrous), with both adult females and males having multiple sexual partners, often within short periods of minutes. If a dominance hierarchy exists, then we would expect that a dominant animal may have greater access to certain other individuals, but this is not clear from wild observations or from one detailed study in captivity (Bateson, 1974). Constant social–sexual play, including homosexual activities by both sexes, indicates that close affiliations and mountings are not necessarily reproductive, but may have a diverse social function that includes strengthening of social bonds, social signalling, or simply play, as known for several great apes (Stanford, 1998; White and Chapman, 1994). Along with dusky dolphins off Kaikoura, New Zealand (Section 4.3) these dolphins have protracted time to rest and socialize while not foraging or feeding, and it is no surprise that they therefore engage in prolonged social–sexual activities away from deep water dangers and food.

In island and atoll-living spinner dolphins, protected bays and lagoons are important habitat for daytime rest and social activities away from shark predation over deep water. There is some indication that size of rest area determines approximate size of group, so that a large bay has a greater carrying capacity than a smaller one (Wells and Norris, 1994). Since there is fluidity in associations, a group that enters a resting bay on one day is composed of somewhat different individuals than on days before and after. Thus, there is considerable overlap in bays used along a larger island such as the Big Island, Hawaii, although individuals appear to have core areas of greater preference.

During the night, a consistent offshore food resource makes grouping an effective anti-predatory strategy and may even allow for cooperative foraging (Benoit-Bird and Au, 2003). Thus, social structure of spinner dolphins associated with a large island habitat, such as the Big Island of Hawaii, seems to be driven by both resource acquisition and anti-predator strategies that lead to a classic fission–fusion society with large, fluid foraging groups at night and considerably smaller, but still fluid, resting groups during the day.

A considerably different social pattern has recently been described for spinner dolphins associated with remote atolls at the western end of the Hawaiian Archipelago, some 2000 km northwest of the main Hawaiian Islands (Karczmarski *et al.*, 2005). In these isolated small atolls, such as Midway Atoll or Kure Atoll, spinner dolphins live in stable, bisexually bonded societies of long-term associates. They are significantly genetically differentiated from the spinner dolphins at the main Hawaiian Islands, with greatly reduced genetic diversity compared to the dolphins at the main islands (Andrews *et al.*, 2006). In the atolls, both males and females form preferential companionships, within and between sexes, and display complex social behaviours such as babysitting. Although the persistence of specific associations (pairs and trios) is stronger for males than females (L.K., unpublished data), the group membership seems remarkably stable. Usually, the entire community of an atoll (approximately 120 dolphins at Kure and 260 dolphins at Midway Atolls) occur in one coherent group, with no obvious fission–fusion and no inter-individual changes in group structure and fidelities from day to day (Karczmarski *et al.*, 2005).

The protected lagoons of the atolls are used daily as resting grounds, and there are well-defined favourite resting sites within each atoll. The dolphins are well familiar with the bathymetry of the area, and use depth contours to travel within the atoll lagoon and to move in and out of the atoll. Interactions between neighbouring atoll communities are rare and generally the dolphins show high geographic fidelity to their specific atoll (Karczmarski *et al.*, 2005). Although movements between atolls approximately 100 km apart were seen, they were infrequent, never involved the entire community or solitary individuals, but rather a subgroup, possibly a basic social unit of about 30–60 individuals. These movements are rare enough that social divergence between neighbouring atoll communities may develop (Karczmarski *et al.*, 2005), but still sufficiently frequent to facilitate gene exchange (Andrews *et al.*, 2006). At Midway Atoll in 1999, a group of dolphins transferred from Kure Atoll, and individuals from the two communities remained socially discrete for several months. Apparent aggression and/or aversion were observed, with the resident community chasing the immigrant group away from primary resting sites into less favourable areas at the atoll's rim, suggesting contest-type competition for favourite habitats (Karczmarski *et al.*, 2005) and even the possibility of territorial behaviour. Three years later, although seemingly integrated into one larger community, the 'residents' and 'immigrants' still showed considerably stronger grouping within their original community memberships.

This social pattern of atoll-dwelling spinner dolphins is considerably different from the pattern observed off the main Hawaiian Archipelago, and seems more akin to such systems as killer whales and long-finned pilot whales (reviewed in Connor, 2000; see also Section 5.2) where individuals remain in long-term groups. These differences in spinner dolphin sociality correspond to the geographic separation and habitat variation across the Hawaiian Archipelago; Karczmarski *et al.* (2005) suggest that geographic insularity and the availability of sheltered shallow-water daytime rest sites influence this difference in overall society structure. In the main Hawaiian Islands, each island provides a mosaic of closely located near-shore environments with several suitable resting habitats in close reach, and each with the capability to hold a certain percentage of a nighttime feeding group. Individuals frequently change daytime resting sites, depending on rest site availability, and group membership varies over time (Würsig *et al.,* 1994b). In far-western Hawaii, suitable resting habitats are restricted to atoll lagoons, limited in size, and separated by large stretches of open pelagic waters with potentially high risk of shark predation. Individuals do not switch resting sites, as it becomes energetically advantageous to spinner dolphins in the remote Hawaiian atolls to remain philopatric rather than travel to other atolls. Thus, there is stability in the community membership and little or no fission–fusion, with long-term inter-individual bonds and complex networks of social interactions. The geographic isolation and small size of remote atolls trigger a process in which the fluidity of the fission–fusion spinner dolphin society is replaced with long-term group fidelity and social stability (Karczmarski *et al.*, 2005).

In the open ocean, spinner dolphins occur in schools of hundreds to a few thousand, often in multi-species associations with pantropical spotted (*Stenella attenuata*), striped (*S. coeruleoalba*) and common (*Delphinus* sp.) dolphins (Perrin and Gilpatrick, 1994; see Section 4.1). The group dynamics and social patterns of the more offshore forms of spinner dolphins remain largely unknown, although considerable geographic variation in the mating system has been suggested based on testis size (Perrin and Mesnick, 2003). These spinner dolphins do not depend on the available resting sites for their daily activities, as they are frequently long distances from the nearest island or atoll. Therefore, we might expect a different pattern of association than those patterns observed off the Hawaiian mainland and atolls.

In summary, three very different patterns of social structure have been described for spinner dolphins. Long-term social bonds and geographic fidelity occur in communities associated with remote far-western Hawaiian atolls, where critical resource (resting sites) is limited but available on very predictable (non-varying) basis. It is advantageous for these individuals to remain at a known and secure location forming relatively small communities of resident dolphins as predicted by our model (Fig. 3.8). Off the main islands of Hawaii, individuals frequently switch daytime resting sites, and association patterns can be characterized as a fluid, fission–fusion pattern. We suggest that the daytime resting sites may not always be available (if they have already been filled by other dolphins); therefore, the more variable availability of daytime resting sites may lead to wider ranging behaviour and more fluid social structure. This pattern fits with our overall model (Fig. 3.7); however as resource availability is less predictable for the main Hawaiian Island spinner dolphins, they display some of the characteristics of more wide-ranging communities (as outlined in Section 4). Finally, offshore spinner dolphins are found in large, often multi-species groups in the open ocean where no daytime resting sites are available. The unpredictable availability of food resources leads these dolphins to display a very different pattern of social organization (as predicted by overall model, see Section 4 for more details).

Most of the research on spinner dolphin social strategies has been conducted around Hawaii. Expanding research to other areas would facilitate an investigation of the role that daytime resting site variability plays in the evolution of spinner dolphin social structure.

3.3. Comparisons with terrestrial mammals

While it is clear from the previous sections that there are differences in social structure in resident dolphin communities, several general trends are evident. Community sizes tend to be relatively small, with individuals mostly associating with only about 100 individuals. Group sizes also tend to be smaller, typically <10 individuals are found within the same group. Foraging is typically either solitary or involves small cooperative groups, and individuals do not tend to form large groups as an anti-predator strategy (Fig. 3.8). This trend does not follow in the case of insular spinner dolphin communities in the far-western Hawaiian atolls, most likely due to other factors such as geographic isolation, the specific nature of the critical resource (shelter habitat rather than food), and the proximity of pelagic waters with both pelagic predators and prey.

Predictable resources have led to long-term residency in many terrestrial mammals as well. Some of the best-studied examples are primates and

African antelope. While comparisons between bottlenose dolphins and chimpanzee social structure have previously been made (e.g., Connor *et al.*, 2000b), we believe it is useful to extend these comparisons between resident delphinids and resident terrestrial mammals in general. However, several major differences exist between terrestrial and marine systems (see Section 1.3.1 for more details), in particular the lack of territoriality (but note a possible exception for atoll spinner dolphin communities, Section 3.2), and the decreased probability of infanticide in the marine system.

Among primates, competition for food resources appears to be an important factor influencing social structure (see Isbell and Young, 2002, for a review). In particular, high levels of contest-type competition (between and within group) can lead to the evolution of social structure resembling that found in resident dolphin groups. Various models of primate social ecology place different emphasis on the role of predation, population density and the costs of dispersal. However, all models agree that clumped distribution of food resources (such as a fruiting tree) can lead to contest-type competition, as individual primates attempt to exclude others from accessing the resource. When specific individuals or groups can exclude others from accessing the resource, aggressive interactions are common and stable dominance hierarchies can evolve. Females cooperate with kin to improve or maintain status within these hierarchies and female philopatry is common (see Isbell and Young, 2002, and references therein for primate socioecology models). Primates that fit this general pattern include vervets (*Cercopithicus aethiops*), baboons (*Papio* sp.), macaques (*Macaca* sp.) and chimpanzees.

Because similar types of primate societies may be driven at least in part by contest-type competition, what is the potential for contest-type competition to occur in resident delphinids? Male herding and sequestering of female bottlenose dolphins represent one of the clearest examples of contest-type competition, where males compete for access to females, and actively attempt to exclude other males from the resource (Connor *et al.*, 1992), although male coalitions are not the only successful strategy in this community (Krützen *et al.*, 2004). Similar contest-type competition may occur in spinner dolphins for access to suitable rest areas, especially in the Hawaiian atolls where groups acted antagonistically towards each other (Karczmarski *et al.*, 2005). It has been expressed (Würsig *et al.*, 1994a) that spinner dolphin groups avoided a rest area already occupied by another group off the Kona coast of Hawaii, and this avoidance could be due to perceived or real competition from those already in the resting area. Another interesting possibility of contest-type competition for profitable habitat occurs in bottlenose dolphins along the southeast coast of the United States. Much of this coastline is fringed with barrier islands, and behind the barrier islands are relatively small, isolated communities of dolphins, best studied in Sarasota Bay. However, a larger ecotype of bottlenose dolphin resides just offshore in these coastal waters. These dolphins range more widely than the inshore dolphins and have different diets (see Section 4.2 for more details). Occasionally, the inshore and coastal dolphins will interact, but usually they are separated by the barrier islands. It is possible, although not tested, that the inshore dolphins exclude the coastal dolphins from the shallower waters, which may represent a safer habitat with more options to avoid predation. Alternatively, the coastal dolphins may exclude the inshore dolphins from the more productive offshore areas. Overall, it is unlikely that contest-type competition plays as important a role in delphinid society as it does in primates, given the difficulties of defending resources in the marine environment, and based on the limited observations made to date.

Many species of African antelope show some similar patterns of residency and sociality, as the resident dolphins described above. Antelopes such as reedbucks (*Redunca redunca*), bushbucks (*Tragelaphus scriptus*) and oribi (*Ourebia ourebi*) tend to feed selectively on specific plant parts found within their small home range. These antelope do not have to range widely to find sufficient resources, and their relatively small group size limits competition for food resources. Their habitat is relatively complex, and they attempt to avoid detection by predators. Female groups do not appear to be territorial, nor do they form long-term bonds. Breeding males appear to hold territories and actively exclude other breeding males (Brashares *et al.*, 2000; Jarman, 1974). Resident dolphins appear to have relatively selective diets, preying specifically on only a few species of fish, which may locally be abundant or profitable to catch. Additionally, individual resident dolphins appear to be highly selective, with individual preferences for prey type and foraging strategy (Mann and Sargeant, 2003; Nowacek, 2002; Sargeant *et al.,* 2007). This dietary selectivity may serve to reduce competition between community members, although this assertion has not been tested. Small African antelope have many strategies to avoid being detected by predators (Caro *et al.*, 2004). Bottlenose dolphins may use similar strategies to reduce predation. In Sarasota Bay, bottlenose dolphins echolocate at lower rates than in other areas (Jones and Sayigh, 2002) perhaps to avoid attracting sharks. Instead, the dolphins appear to use passive acoustics to find prey (Gannon *et al.*, 2005) and relatively rarely echolocate.

Three hypotheses have been proposed to explain the evolution of group living in carnivores, and all relate to the acquisition of territories (Bekoff, 2001) and thus are unlikely to give much insight into the evolution of social groups in delphinids. However, once carnivores form groups, individuals can benefit from anti-predatory strategies and/or cooperative exploitation of resources, and these studies may assist us in examining social strategies in delphinids. Many of the cat species are solitary, as competition for food resource likely prohibits group formation. Resident delphinids appear to be predominantly individual foragers, with little to gain from cooperative foraging. However, as dolphins face much lower transportation costs than terrestrial species they may be able to forage solitarily but then aggregate for social behaviour or anti-predator protection, while terrestrial carnivores which forage solitarily usually remain solitary except for breeding.

Resident dolphins tend to live in relatively small communities composed of small fluid groups. These dolphins do not range widely, probably due to the reliability of food resources. Although food resources are reliably located, they are not abundant and therefore the community size is limited and individuals are more likely to benefit from solitary foraging. In this protected inshore habitat, they rely on their ability to hide and avoid predators, rather than using grouping as an anti-predator strategy. The characteristics of this habitat result in few benefits to forming large groups, and many benefits to being solitary or in small groups. There are relatively few advantages to females forming long-term bonds, for cooperative foraging, babysitting or predator avoidance. This permits the possibility that males may be able to sequester reproductively active females, and prevent other males from mating with her. When competition for females is high, males may benefit from cooperating to herd females, as has been observed in bottlenose dolphins. Characteristics of the habitat of these resident dolphins are similar to some African antelope and primates such as vervets, baboons, macaques and chimpanzees. Explicit examination of the role of contest versus scramble-type competition in resident delphinids and further investigation of anti-predator strategies may increase our understanding of the role of ecological characteristics in the evolution of resident delphinid social strategies and their similarities with terrestrial mammals.

4. WIDE-RANGING COMMUNITIES

When resources such as food are unpredictable or at lower concentration, individuals must range further to find sufficient resources. The lability of resources in offshore areas may be due to fluctuations in oceanographic conditions over varying time scales such as the short-term presence of eddies, seasonal fluctuations or long-term variability such as El Niño Southern Oscillation (ENSO) events. The home range of individuals will depend on the persistence and severity of these fluctuations. However, it is likely that predation risk and foraging habitat are less predictable over the entire range, and individuals are less likely to have intimate detailed knowledge of every aspect of their home range. Thus, it may be more difficult to reduce predation risk, simply by avoiding high risk areas. In fact, in these situations, predators are likely to be as mobile as their prey and be less predictable in distribution. Additionally, most of these wider ranging communities are found in more open unstructured environments where there are few places for refuge, and forming groups may be the only reliable (or available) anti-predator strategy (Fig. 3.10).

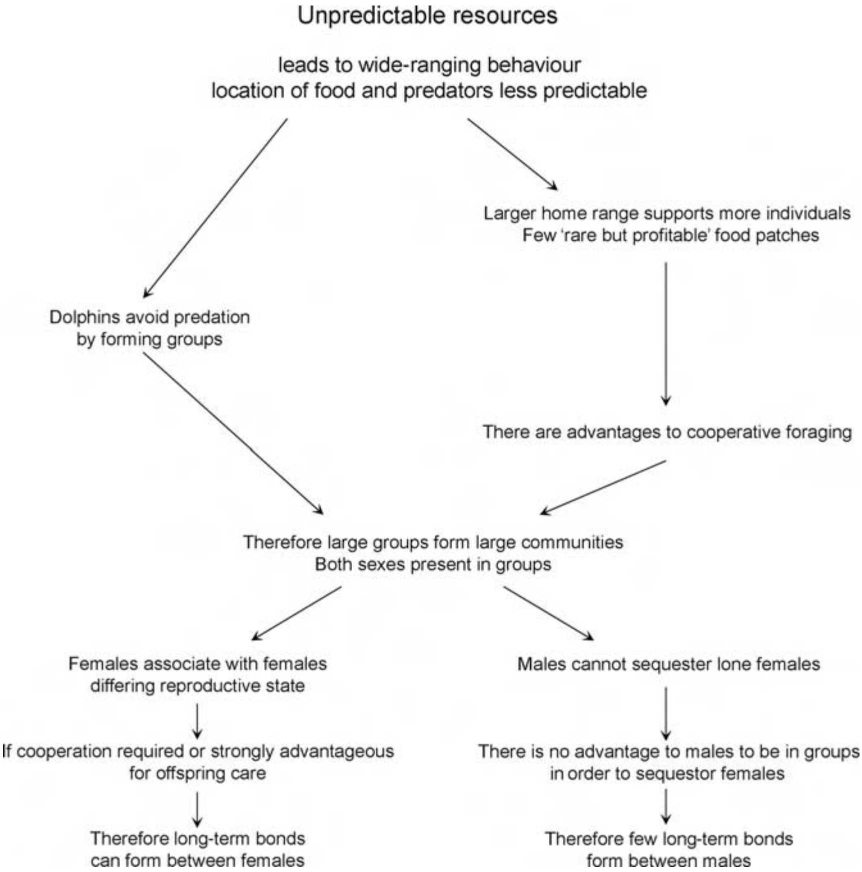


Figure 3.10 Model conceptual framework describing the influence of unpredictable resources on delphinid social strategies. Large group sizes are favoured to reduce predation risk and access food resources. Within these large groups, male bonds are unlikely to form; however, females may form long-term bonds if cooperation between females increases the survival of their offspring.

Larger home ranges are likely to support a greater number of individuals; however, prey is often found in larger schools with vast areas in between schools with little to no prey. In these situations, cooperative foraging and herding of fish or cephalopod schools may be advantageous. When prey schools are very large, foraging competition may be reduced as food is superabundant. If cooperative foraging is present, then individuals may form long-term bonds either with kin (kin selection) or non-kin (reciprocal altruism). These foraging and anti-predator strategies may lead to larger communities of larger groups of dolphins.

In these situations, males and females receive benefits from being in groups, and the observed groups are often very large with males and females present. These large groups make it difficult for a male or a small group of males to sequester a female throughout an entire oestrus cycle, and polygynandry is the most likely mating strategy. As it is difficult to sequester females, there is little advantage to forming strong bonds between males, and male–male associations may be more weak and labile. In contrast, females may form long-term strong bonds if cooperation is required to successfully raise offspring, as has been suggested for sperm whales (Whitehead, 1996). However, if cooperative foraging does not occur, or does not require extensive coordination of individuals, then females (and males) may form no long-term associations, but simply display many short-term affiliations with a large number of individuals.

4.1. Eastern Tropical Pacific dolphins (*Delphinus* and *Stenella* sp.)

In the open ocean, the smaller delphinids, such as common, spinner, striped and spotted dolphins, tend to be in very large groupings of hundreds to thousands. Especially in the tropical Pacific, there is a tendency for several species to travel together, and it has been hypothesized that such multispecies aggregations may more efficiently detect sharks while feeding at different depths or time of day. For example, pantropical spotted dolphins tend to feed during daytime and spinner dolphins at night, so it has been surmised that aggregations composed of the two species essentially trade times of increased vigilance, while muting competitive interactions related to finding and securing food (Norris and Dohl, 1980). There is a general but not complete tendency for the larger delphinids, such as Risso's dolphins, pilot whales and false killer whales, to occur in smaller schools, and it is generally surmised that this is possible for them as they are not as vulnerable to shark predation due to their larger size (summarized by Wells *et al.*, 1999a).

Little is known about community structure in these large, wide-ranging groupings of offshore dolphins. While techniques, such as photo-identification and genetic analysis of biopsy samples, have revealed great insight into the lives of coastal dolphins, these techniques are difficult to apply to offshore animals. It is difficult and expensive to locate and follow groups of dolphins over long periods. It is also difficult to apply photo-identification techniques to large open populations. Therefore, our knowledge of offshore dolphin societies is much restricted. Insights into offshore dolphin sociality have come from brief observations and inferences drawn from morphometric analysis of by-caught dolphins (e.g., Perrin and Mesnick, 2003; Pryor and Kang Shallenberger, 1991).

Open ocean dolphins travel great distances of hundreds (to low thousands) of kilometres, often in remarkably short periods (Reilly, 1990). It is a widely held view that large scale travel by large schools allows efficient uptake of limited resources in the relatively low productivity of tropical seas, much as large herds of Serengeti Plains migrating grazers (Jarman, 1974) need to keep moving so as not to deplete their resources in one area. However, another reason for moving may have to do with not attracting predators such as large sharks and (potentially) killer whales to a specific location, as has been suggested for many systems (Brown *et al.*, 1999; Ripple and Beschta, 2004). Dolphins in the open ocean travel together as a mixed sex and age school, and it is likely that all social–sexual interactions go on within the large school, but with subgroupings of certain age and sex spread throughout the school, and with fission–fusion interactions among subgroups (Dohl *et al.*, 1986; Pryor and Kang Shallenberger, 1991).

Most dolphins of the open ocean show muted sexual dimorphism, indicative of a polygynandrous (or multi-mate) society. Recently, Perrin and Mesnick (2003) provided an evaluation of two geographic forms of spinner dolphins, the highly sexually dimorphic eastern form, where adult males develop a tall forward canted dorsal fin and prominent postanal keel; and the whitebelly form that shows some slight sexual dimorphism (see Section 3.2 for details on different forms of spinner dolphins). They reanalysed morphometric data (Perrin *et al.*, 1991) in conjunction with testes sizes (Perrin and Henderson, 1984) in these two forms, from an extensive database of thousands of animals killed in the tuna-purse seine fishery. The sexually dimorphic eastern form has small testes, while the more monomorphic form has large testes, and the combination of data allows the reasonable interpretation that there is more polygyny (i.e., males competing for access to females in some manner) in the eastern form, and more of a multi-mate strategy of potential sperm competition (Brownell and Ralls, 1986; Kenagy and Trombulak, 1986) in the whitebelly form. The eastern spinner form lives in one of the most productive tropical ocean regimes, just north of the equator (Ballance *et al.*, 1997). Perrin and Mesnick (2003) hypothesize that the high productivity may allow females to form close-knit, long-term bonds (this supposition lacks observational data at this point), and may have led to males needing to compete physically for females. Furthermore, the high productivity may have released males from foraging time to make polygynous competition possible. In the less productive waters occupied by whitebelly spinners, perhaps female bonds are less tight, there is more overall coordination of protection from predators and foraging together, and a polygynandrous strategy of multi-mating (sperm competition) is the norm. The least sexually dimorphic form of spinner dolphins occurs in Hawaii, other island and atoll situations, and much of the western and southern tropical Pacific. In Hawaii, it has also been suggested from behavioural observations (Johnson and Norris, 1994) that the system tends towards polygynandry (see Section 3.2).

Beyond reasonable inferences taken from morphological data on sexual dimorphism and testes size, there is little direct information about social strategies in slim-bodied open ocean pelagic dolphins such as spinner, pantropical spotted and common dolphins. High resolution photography from the air shows that such schools have subgroup structure with partial separation of reproductive females, apparent adult males and mixed age/sex groupings (Scott and Perryman, 1991). It is unknown how long associations last, beyond the mother–calf association. However, it is unlikely that there are tight bonds among the members of all or most of the school, and fission–fusion associations exist within the overall school.

With formation of a large school the entire life of an individual may remain within that ever-moving large community, broadly analogous to the migration of wildebeest (*Connochates tauriuns*), caribou (*Rangifer tarandus*) and human hunter-gatherer tribes (Berger, 2004). In the large school, cooperation can develop, although we presently do not have the behavioural details to substantiate this likelihood of cooperation, nor knowledge of persistence of long-term bonds beyond the mother–calf bond.

While there is limited information available about the foraging behaviour, social structure and predation risk of offshore Eastern Tropical Pacific dolphins, what is known appears to support the proposed framework. These dolphins form very large groups and range over wide areas. In the future, detailed information on the foraging behaviour, social structure and predation risk faced by dolphins of these communities would provide a valuable test of this proposed framework.

4.2. Coastal bottlenose dolphins (*Tursiops* sp.)

Bottlenose dolphins (*T. aduncus* and *T. truncatus*) are found in coastal waters, often close to shore, but also offshore of barrier islands. The inshore and offshore ecotypes can be differentiated by morphological features (including larger body size in the offshore type), cranial morphology, haematology and parasitic infections (Hersh and Duffield, 1990; Van Waerebeek *et al.*, 1990; Walker, 1981). Genetic differences have been found in both the mitochondrial and nuclear genome between offshore and inshore dolphins, further indicating their reproductive isolation from each other (Hoelzel *et al.*, 1998). The offshore ecotype has a relatively cosmopolitan distribution, found in the Atlantic, Pacific and Indian oceans (Duffield *et al.*, 1983; Ross, 1984; Ross and Cockcroft, 1990; Van Waerebeek *et al.*, 1990; Walker, 1981).

In comparison to the inshore ecotype (see description in Section 3.1), relatively few studies have been conducted on the offshore ecotype of bottlenose dolphins. This is in large part due to the difficulties of studying these wide-ranging dolphins, which do not stay within a small, logistically manageable study area. Photo-identification studies have been initiated off the coast of California (Defran and Weller, 1999; Defran *et al.*, 1999) and Florida (Caldwell, 2001); however, none of them have been able to resight routinely either large number of individuals or re-identify them throughout their range. It has also been difficult to estimate the number of dolphins in these communities.

Prey preferences of coastal bottlenose dolphins have not been studied in the same detail as inshore bottlenose dolphins, but some differences have been noted. Off Florida, stomach contents of stranded dolphins show that coastal and offshore specimens have higher proportions of cephalopods than inshore forms (Barros and Wells, 1998). Off the California coast, bottlenose dolphins appear to prey predominantly on surfperch (*Embioticidae* sp.) or croakers (*Sciaenidae* sp.; Bearzi, 2003), whereas off South Africa, deep-water reef fish were an important part of the diet of offshore forms (Ross, 1977). Predation risk is poorly understood in coastal areas, but it is likely that these dolphins are at least occasionally preyed upon by sharks (Heithaus, 2001b) and killer whales (Jefferson *et al.*, 1991), and these coastal habitats provide few refuge opportunities.

Although the data are sparse, offshore bottlenose dolphins tend to display a very different pattern of residency and social structure than the more inshore bottlenose dolphins (described in detail in Section 3.1). These more offshore bottlenose dolphins appear to be found in much larger open communities which range widely and show relatively few long-term associations. For example, bottlenose dolphins off California (an area without an inshore bottlenose dolphin community due to the lack of barrier islands) are typically found in groups of 10–20 or more dolphins (Bearzi, 2003; Defran and Weller, 1999). Very few individuals were resighted with previous associates, indicating weak and fluid association patterns (Weller, 1991). In the area off San Diego, it was estimated that approximately 250 bottlenose dolphins were present annually; however, low resighting rates indicate that this is only one portion of a much larger open population (Defran and Weller, 1999). Movements of identified dolphins support this idea, as several long-distance re-sightings were recorded, including a rapid movement of dolphins identified off San Diego which were photographed north of Santa Barbara, some 286 km further north, only 14 days later (Defran and Weller, 1999; Defran *et al.*, 1999).

Studies of coastal bottlenose dolphins off the coast of Jacksonville, Florida, show a similar pattern to those observed off California. In the coastal waters of Jacksonville, bottlenose dolphins were observed in groups of about 17 individuals that showed no signs of residency in the area. Some of the dolphins photographed off Jacksonville were photographed 200 km further north off Hilton Head, South Carolina, while others were photographed 440 km further north off Myrtle Beach, South Carolina. Some individuals were sighted together on different occasions; however, data were too sparse to quantitatively analyse social structure and most individuals did not display long-term associations (Caldwell, 2001). In contrast to the California coast, barrier islands exist along the east coast of Florida, and a different community of dolphins were observed behind the barrier islands. Inshore and coastal dolphins did not interact, and genetic studies of these dolphins indicated little mixing. The social structure of the inshore bottlenose dolphins near Jacksonville more closely resembles other communities of inshore groups (see Section 3.1; Caldwell, 2001).

Detailed movement patterns of a few offshore type bottlenose dolphins have been described based on satellite telemetry. Wells *et al.* (1999b) tracked two males that had initially stranded along Florida's coast after they were successfully rehabilitated. After release, one male moved over 2000 km in 43 days from the Gulf of Mexico to offshore of Cape Hatteras, North Carolina. The other male moved 4200 km in 47 days from Cape Canaveral Florida, across deep water (5000-m maximum depth) to northeast of the Virgin Islands. In contrast, two offshore bottlenose dolphins that were captured, satellite tagged and released off eastern Australia remained over shallow but offshore water (typically <50 m) and rarely dived below surface waters (most dives were <5 m; Corkeron and Martin, 2004).

Bottlenose dolphins are found in coastal waters in other parts of the world, including the east coast of South Africa. Here, Indo-Pacific bottlenose dolphins (*T. aduncus*) appear to show similar social structure to those observed off Florida and California, with large groups several tens to a few hundred individuals which range widely and do not show clear patterns of long-term associations (L.K., unpublished data). However, it is much more difficult to study wide-ranging communities as research effort must be spread over a far greater geographic area. Thus, our understanding of dynamics in these communities is much more limited and additional social structure may be present, but undetected at this time.

In Bahamian waters, there are few inshore locations, but a community of coastal ecotype of bottlenose dolphins (*T. truncatus*) has been well studied in the shallow waters of Little Bahama Bank. Their physical characteristics, social structure, ranging behaviour and site fidelity are similar to the inshore bottlenose dolphins of Florida (Rogers *et al.*, 2004; Rossbach and Herzing, 1999). Groups are typically composed of 3–5 dolphins, and show fission–fusion. The strongest bonds were between mothers and calves, while female associations varied with reproductive state. Long-term associations were formed by some males (Rogers *et al.*, 2004) and appear to be kinship based (Parsons *et al.*, 2003). This community appears to resemble the inshore bottlenose dolphin pattern despite its offshore location. This group of dolphins tends to forage individually on benthic prey (Rossbach and Herzing, 1997), suggesting that when individuals forage on solitary prey, dolphins do not form large cooperative groups, as observed in other offshore bottlenose dolphin communities.

Bottlenose dolphins are also found further offshore in neritic and pelagic waters. Little is known about the ranging behaviour, diet, predation risk or social organization of these dolphins. Group sizes are typically smaller (Connor *et al.*, 2000b) than some of the other offshore dolphins (see Section 4.1), but it is difficult to draw any conclusions from these differences.

The behaviour of offshore bottlenose dolphins (*Tursiops* sp.) provides further support for this framework; however, many details are lacking to fully test the proposed framework. The work initiated off California and Florida will provide a valuable test of this hypothesis. The observations of bottlenose dolphins off the Bahamas provide valuable support for this framework as the association patterns of these dolphins resemble the patterns observed in inshore bottlenose dolphins (see Section 3.1) despite their offshore habitat. However, bottlenose dolphins off the Bahamas and in Sarasota and Shark Bay appear to forage individually on predominantly non-schooling prey which tend to be predictably available (Mann and Sargeant, 2003; Nowacek, 2002; Rossbach and Herzing, 1997; Sargeant *et al.,* 2007). In contrast, the framework proposed by Wells *et al.* (1999a), which focused on habitat complexity and predation pressure, suggests that the bottlenose dolphins off the Bahamas should form large groups to avoid predation in their open ocean habitat.

4.3. Dusky dolphins (*Lagenorhynchus obscurus*)

Dusky dolphins occur discontinuously on both sides of southern South America (in Peru, to as far north as about 7°S; in Argentina, to at least about 38°S), the south-western coast of South Africa, the south island and southern half of the north island of New Zealand, occasionally off Tasmania and southern Australia, and off several south Atlantic and southern Indian Ocean Islands (Brownell and Cipriano, 1999; Van Waerebeek and Würsig, 2002). They are a semi-pelagic species, preferring water no deeper than about 2000 m, generally near shore, on or near continental or island submarine shelves. They are found over expansive non-pelagic shelves between New Zealand and the Chatham Islands (Gaskin, 1968), and >200 km from shore east of Argentina (Dans *et al.*, 1997). Yet they also occur in bays and inlets, although only as seasonal residents and not as year-round resident communities (Würsig and Würsig, 1980 for Golfo San José, Argentina; Markowitz *et al.*, 2004 for Admiralty Bay, New Zealand). Therefore, while we place them among the 'wide-ranging' communities, they have elements of seasonal residency in some areas and elements of intermediate-ranging patterns, as will be described in more detail below. Their closest generic relative is the northern hemisphere Pacific white-sided dolphin, and it is presently unclear how closely they are related to other southern hemisphere and North Atlantic *Lagenorhynchus* species (Cassens *et al.*, 2003; Leduc *et al.*, 1999).

Dusky dolphins are a small delphinid, generally <200-cm long (with some specimens off Peru slightly >200 cm). Males are slightly larger than females at the same age, and there is a tendency for males to have thicker and more curving dorsal fins than females. This somewhat muted sexual dimorphism hints at a polygynous society, but details are unknown.

Dusky dolphins tend to feed on fishes and squid of a large variety of species, but generally with prey body lengths less than about 30 cm (Cipriano, 1992). They are gregarious wherever they occur, in groups from less than one dozen to well over 1000 individuals (Würsig *et al.*, 1997). Deep-water sharks, such as broadnose sevengill, great white and shortfin mako, probably pose risks in much of their range (Crespi-Abril *et al.*, 2003; Heithaus, 2001b; Van Waerebeek and Würsig, 2002); and killer whales take them off Argentina (Würsig and Würsig, 1980) and the east coast of the south island of New Zealand (Constantine *et al.*, 1998). Large group sizes may be at least a partial response to predation, and use of near shore habitats (see below) may minimize both shark and killer whale attacks (Würsig and Würsig, 1980).

Dusky dolphin foraging and social strategies have been studied in some detail in shallow waters of Golfo San José, Argentina (Würsig, 1982, 1986; Würsig and Würsig, 1980), and Admiralty Bay, Marlborough Sounds, New Zealand (Markowitz, 2004; Markowitz *et al.*, 2004; McFadden, 2003), as well as in deep waters of the Kaikoura Canyon, New Zealand (Benoit-Bird *et al.*, 2004; Markowitz, 2004; Würsig *et al.*, 1997). Group structures and foraging strategies are remarkably different in these two disparate habitats.

In shallow waters (to about 60 m) off Argentina, dolphins in summer have a marked fission–fusion society. Approximately 300 dolphins live in the community of Golfo San José and groups range about 20–100 km d^{-1} usually in zigzag movements, as they search for food. However, they may move to other adjacent areas, up to about 300 km away, for days to weeks at a time (Würsig, 1982). The general pattern for the community is to occur in about 30 small subgroups (6–10 dolphins) in early morning, with the subgroups covering an area over 100 km^2 as they slowly travel within about 1 km from the nearest other subgroup. It appears that when one subgroup finds a school of fish (anchovy, *Engraulis* sp.), aerial leaping behaviours increase, birds aggregate and dolphins from other subgroups recruit to that area. It is thus apparent that dolphins detect activities of other groups, and perhaps communicate, across distances approximating 1 km or more. The group size grows, at times with all 30 or so subgroups coalesced after one or more hours. Dolphin subgroups appear to make decisions as to which other subgroups to approach, presumably by an assessment of intensity of activity with fish and birds. Some subgroups that begin herding (or baitballing) are not approached, and these activities tend to die out after 10–15 min (sometimes less), suggesting dolphins require greater group size to efficiently herd the prey into a tight baitball that is stable over time. Typically, dolphins that herd fish do not begin to feed until the fish school is tightly balled. Dolphins rapidly move under and around fish schools, often emitting bubble blasts from their blowholes to help herd the school. They use the surface as a wall against which a fish school is pinned (Würsig and Würsig, 1980).

As feeding progresses and group size becomes larger due to fusion of smaller subgroups, dolphins display activities such as highly acrobatic leaps (Fig. 3.11), head-outs (raising their heads out of the water, without jumping clear of the surface), chasing each other and copulating (including homosexual activities within both sexes), and mouthing or rubbing a wide variety of objects including the legs of marine birds, large fishes, small sharks, humans in the water, the side of a research boat and inanimate floating objects such as kelp or debris. These activities after intense feeding are most frequent when most or all dolphins within an area are together, and this high level of sociality can last for up to an hour or more. Generally late in the afternoon, dolphins fission back into smaller subgroups, and stay in small subgroups, close to shore, until the next day.

It is surmised that this diel cycle occurs so that at night dolphins rest in shallow waters close to shore, away from shark and killer whale predation and in groups not easily discovered. Fissioned groups thus allow for efficient rest but also allow for enhanced capability of finding food in the morning, as they range over a wide area. Fusion of groups allows for enhanced herding and feeding, and during/after feeding the social activity is probably important for social bonding. During daytime feeding, mothers and calves tend to feed early on, but segregate from the feeding-socializing group as play and mating activities increase. It is unclear whether there is strong sexual segregation in subgroups, but there appears to be a tendency for mothers and calves to form separate subgroups (or nursery groups); as well as some subgroups to be composed of all males and others to be of mixed sex and age

Figure 3.11 Dusky dolphins *Lagenorhynchus obscurus* are highly aerially acrobatic. Here a male chases a female off Kaikoura, New Zealand. Coordinated, rapid salmon-like leaps of this kind are often directly followed by a quick copulation. (Photo courtesy of B. Würsig.)

(Würsig and Würsig, 1980). While subgroups tend to have at least some different memberships from day to day, one pair of dolphins that was marked together in one subgroup in 1975 was sighted together almost eight years later (Würsig and Bastida, 1986).

Among dusky dolphins in winter in Argentina, there is less fission–fusion (and lower occurrence of Argentine anchovy), and most subgroups of 6–10 animals stay in shallow water day and night. It is surmised that winter non-aggregating feeding is of a more individual than highly cooperative nature (Würsig and Würsig, 1980), but more work needs to be done to adequately describe the social patterns of this community throughout the annual cycle.

Off New Zealand, dusky dolphins occurring in winter in shallow waters of Admiralty Bay feed largely on schooling pilchards (*Sardinops sagax*), yellow-eyed mullet (*Aldrichetta forsteri*) and sprat (*Sprattus antipodum*), also in association with birds (Würsig *et al.*, 2007). A community of about 150 dolphins at any one time is present in Admiralty Bay, but typically split into subgroups of 3–12 animals (Markowitz, 2004). In this locale, dolphin groups range little on a daily basis, moving within an area of only about 10–20 km in diameter. Unlike in Argentina, there may be no concerted effort to move fish schools towards the surface, and much feeding appears to occur deeper than 10 m below the surface. This may be due to different behaviours of the dolphins or their prey. Furthermore, there is no consistent and clear fusion of subgroups, although they move towards each other at times. Certain known individuals return to Admiralty Bay year after year (Markowitz, 2004). It is presently not known why only particular dolphins make the trip, and it has been suggested that use of this winter foraging habitat may be a cultural phenomenon passed from one generation to the next among some, but not all, dolphins of the larger society (Whitehead *et al.*, 2004).

Dusky dolphins occur throughout the year in and near the Kaikoura Canyon, on the east coast of New Zealand's south island. This is an open ocean environment, not unlike non-bay coastal areas of Hawaii, as described for spinner dolphins. There can be between 500 to several thousand dusky dolphins in the waters near Kaikoura at a time, the largest groups usually in late autumn to early winter. Here, dolphins move north and south along shore, travelling back and forth in an approximate daily range of 20–50 km, but sometimes up to 100 km. Different dolphins are observed near Kaikoura in the summer and winter. Some of the dolphins identified in the summer near Kaikoura have been photographed in winter in Admiralty Bay, several hundred kilometres to the north. Near Kaikoura, group sizes are highly variable, from subgroups fewer than one dozen to well over 1000 animals in one cohesive school. Subgroups, composed of nursery groups, apparently all males, and others of mixed sex and age, often travel on the periphery of the larger group of several hundred animals, as far as 100 m to 10 km or so from the main group. There is no strong or time-predictable fission–fusion (Würsig *et al.*, 2007).

During the day, dusky dolphins near the Kaikoura Canyon travel back and forth within several kilometres of shore, rest and socialize. There is very little daytime feeding, with baitballing and associated birds seen only rarely; on average less than once per year in the past 10 years of research. At dusk, dolphins spread out into small subgroups, separated from others by about 20–100 m, but stay cohesive as a school, all travelling in the same direction. They head into deeper water, generally along the escarpment of the Kaikoura Canyon. There is a well-developed diel-vertically migrating deep-scattering layer that rises towards the surface in these oceanic waters. Sonar used to track both the deep-scattering layer and individual dolphins (Benoit-Bird *et al.*, 2004) shows that dusky dolphins do not begin to feed until the layer is within 130 m of the surface, and prefer to feed at depths <100 m. The deep-scattering layer-associated organisms are available for the dolphins throughout all or most of the night and then the dolphins return closer to shore just before or during dawn, when the deep-scattering layer descends below their preferred diving range. We suspect that the daytime preference for shallow water is to avoid the higher risk of predation in deep water (as suspected for island-associated spinner dolphins, Section 3.2).

While dusky dolphins off Argentina have intensive bouts of social–sexual activity closely linked to a post-prandial state in both Admiralty Bay and off Kaikoura, such bouts are less intense and are spread throughout the daytime in sporadic brief (10–20 min) social activities. However, the amount of socializing during the night for any of the three studied areas is not known.

The mating system or systems are unknown for dusky dolphins. Slight sexual dimorphism suggests that males may compete for access to females and that some males gain more copulations of females in oestrus than do others. However, the sexual dimorphism is indeed so slight that the system may tend more towards poygynandry, or multi-mate, and that sperm competition may be important.

In summary, dusky dolphins feed both in daytime on schooling fishes and at night on mesopelagic fishes and squid, depending on habitat and food availability patterns. In Argentina they have a fission–fusion society related to foraging and refuge from predation risk, but do not have such strong and constantly fluctuating subgroup membership in the shallow- and deep-water habitats in New Zealand. In deep water off the Kaikoura Canyon, it is probably of advantage to remain in a large school both day and night, since sharks and killer whales are present in these oceanic waters even though the dolphins are quite close to shore (generally within 10 km). In both the Argentine and Admiralty Bay inshore situations, groups can be quite small without overt fear of predation. In Argentina, the smallest groups, of generally fewer than 12 animals, stay very close to shore to rest and socialize, and have been seen to retreat into the surf zone when killer whales approach. However, the fission–fusion nature of feeding societies, especially so during summer in Argentina when feeding on schooling fishes, indicates that the larger group size may be important to efficient feeding at least as much as to predator detection/avoidance strategies.

Overall, dusky dolphins show at least three different grouping patterns: Off Kaikoura New Zealand deep-canyon waters they occur as a large seasonally resident society; off Argentina over an expansive continental slope, they occur in strong fission–fusion from small to large groups, with much travel; and in Admiralty Bay New Zealand, they occur in small seasonally resident groups. These patterns appear to track our general framework very well. In Argentina, prey are unpredictably distributed and dolphins need to range widely to find enough food. They form large groups related to apparent cooperative foraging, but split into small groups and move nearshore in order to rest at night, presumably to minimize predation while they do not need to be in open water areas to feed. The large daytime groups may also be of advantage to help detect predators, and to react faster/ more efficiently than in small groups in open water, but this is presently unknown. Off Kaikoura, the large school envelope both day and night would seem to allow greater vigilance of predators and may help enhance long-term bonds and cooperative foraging. Here, prey are predictably found at the edges of the Kaikoura Canyon, and movements are restricted to within about 50 km along the shore. In the Admiralty Bay situation, predictable food resources seem to be available in the complex inshore environment of the area. Dolphins can hide nearshore in reaction to predators, but may be limited to the small groups sizes in which they are found because of limits of food in this smaller-extent environment. Interestingly, many of the same dolphins that feed at night in the Kaikoura Canyon in summer in large groups move to Admiralty Bay to feed in daytime in winter in small groups. They thus change strategies and grouping patterns in flexible manner, and generally consistent with the framework.

4.4. Comparisons with terrestrial mammals

As described above, wide-ranging dolphins tend to be found in larger groups than more resident dolphins, although much variation exists. Typically, these dolphins feed on sparsely distributed but abundant food, thus reducing competition. Therefore, it is beneficial for individuals to form large groups to increase the likelihood of detecting prey patches and or reduce predation risk. Within these large groups, social affiliations are likely, however, researchers have found these difficult to document.

By comparison, primate food resources rarely fit the pattern of rare but abundant and instead high levels of competition (either scramble or direct) restrict group sizes (Isbell, 1991; Isbell and Young, 2002). Travel costs are high for primates, and consequently wide-ranging behaviour is rarely observed (Isbell *et al.*, 1999). However, patterns of social structure and movement similar to that of wide-ranging delphinids can be observed in large-grazing ungulates in open grasslands. Jarman (1974) suggested that among African antelopes, those found in larger groups had a non-selective diet of a broad range of grasses, fled or counterattacked predators and had large body size. Their need for large quantities of low-quality food, which is often seasonally variable, led to large home ranges on the open savannah. However, when grasses are available they are typically fairly abundant, and therefore competition for grass patches is relatively rare. Additionally, as there are relatively few places to hide in the African savannah, increased group size is an effective way to reduce predation risk. Recent quantitative analysis of social structure and movements in African ungulates indicated that pattern of large body mass, non-selective diet, large group sizes and anti-predator behaviour holds true even when phylogenetic effects are removed (Brashares *et al.*, 2000).

Home range size often scales with body size (Jetz *et al.*, 2004; LaBarbera, 1989; Peters, 1983) as larger animals require greater food resources. However, attempts to correlate home range with body size in macropod marsupials revealed an interesting deviation, with home range size closely associated with climate (especially annual rainfall) rather than body size. Female marsupials living in the rainforest with high-annual rainfall had small home ranges and foraged on predictable food resources. In these habitats, males had larger ranges, which overlapped with the home ranges of several females indicating that females were minimizing energetic costs related to travel, while males maximized exposure to the number of females (Fisher and Owens, 2000). In contrast, females living in the Australian desert, in areas with low-annual rainfall, had large home ranges and tended to forage on much less predictable resources. Males had similar sized home ranges as did females, perhaps indicating that these home ranges cannot be increased because of travel costs and males were not able to increase contact with more females (Fisher and Owens, 2000). In some cases, these species will form mixed sex groups, although sexual segregation is also common (Fisher and Owens, 2000; MacFarlane and Coulson, 2005).

The unpredictable nature of food resources of the Australian desert and the African savannah shares some similarities with the open ocean. While ungulates and macropod marsupials have often been considered convergent dominant herbivore species (Fisher and Owens, 2000), delphinids are clearly not herbivores. However, patches of grasslands and large fish schools do have some remarkable similarities. Locations of both resources can be patchy, unpredictable and ephemeral. The effect of a small-localized rain shower on an arid location can rapidly lead to plant growth, providing high yield resources in relation to the surrounding area. Grazers can then able to deplete the patch, or the patch dies back naturally without further rainfall. Similarly, the arrival of a school of fish can suddenly increase food availability in a discrete location and disappear quickly as it is either consumed by predators or moves to another location (or, for smaller delphinids, below their preferred dive depth). In these situations, resources are locally abundant and competition between group members (either herbivores or delphinids) is reduced, and therefore relatively large groups can form.

In contrast, terrestrial carnivores rarely encounter highly dense but sparsely distributed food patches. While food resources are patchy, they are rarely sufficiently abundant that competition could be reduced. Instead, competition for these resources restricts group sizes and in most cases constrains carnivores to a solitary lifestyle (Geffen *et al.*, 1996; Gittleman, 1989). Approximately 10–15% of the species within the carnivore class are social (live in groups outside the breeding season); however, most live in relatively small groups (<10 members; Gittleman, 1989). Although groups cooperating to hunt can bring down larger prey than solitary individuals, even large prey represent a limited food resource and competition for food resources likely limits these groups from becoming larger (Creel, 1997; Geffen *et al.*, 1996). Travel costs are likely to limit terrestrial carnivores from increasing their ranges to support more individuals in a group. In contrast, low travel costs for cetaceans permit movement to disparate but new superabundant food patches, and delphinid grouping can occur on scales generally inaccessible to terrestrial carnivores.

While there is considerable support that large group sizes are an adaptive response to living in open habitats with unpredictable food resources (e.g., Brashares *et al.*, 2000; Fisher and Owens, 2000; Jarman, 1974), Gerard *et al.* (2002) argue that observations of increased group size in open habitats is an emergent property, resulting simply from the increased visibility of other groups in open habitat and an attraction between individuals in different groups. In closed and complex habitats, individuals and groups are less likely to detect each other and therefore groups remain small (including solitary individuals). In open habitats, individuals can perceive another individual or group at greater distances and therefore are more likely to join, resulting in larger group sizes. While some observations of terrestrial ungulates support this hypothesis (Gerard *et al.*, 2002), it is unclear if similar trends would occur in the open ocean, where perception of other groups is likely aural (acoustic) rather than visual.

5. INTERMEDIATE-RANGING PATTERNS

The observed social strategies of the delphinids described above (Sections 3 and 4) clearly indicate that even within a species a great deal of variation occurs. While it is possible to fit some species into the broad categories of resident and wide-ranging patterns, other species clearly do not

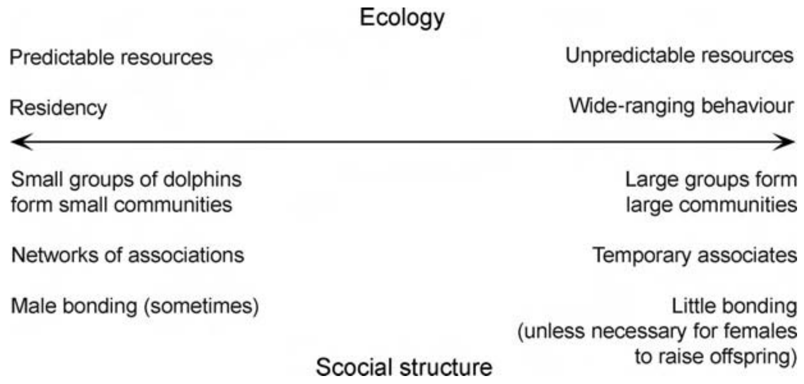


Figure 3.12 The influence of ecology, in particular the predictability of resources on the evolution of social structure in delphinids, such as ranging behaviour, group size and formation of associates and long-term bonds.

fit these patterns. We perceive that resource availability exists in a graded continuum from predictable to extremely variable and less predictable (Fig. 3.7). Therefore, we expect that delphinid ranging patterns, which we believe are determined in large part by resource availability, are also likely to vary along a graded continuum (Fig. 3.12). At intermediate-ranging patterns, individuals form mid-sized groups, which reduces intra-group competition for resources while still providing protection against predation. It is within intermediate-ranging patterns of delphinid groups that we may find the strongest support and challenges to our proposed hypothesis, as examinations of exceptions to the rule often result in different interpretations of a dataset (e.g., Henzi and Barrett, 2003).

Killer whales (Section 5.2) may be one of the most important exceptions in this respect, as it has been suggested that they face limited or no predation pressure, especially as adults. Additionally, many groups are strongly kin based, and we expect that cooperation among kin may play a much larger role in group dynamics rather than the repression of competition.

5.1. Humpback dolphin (*Sousa* sp.)

Humpback dolphins (genus *Sousa*) inhabit coastal waters of Indian and western Pacific oceans and tropical West Africa. They are medium-sized (up to 280 cm in length) and robust, with a maximum weight of 250–280 kg (Ross *et al.*, 1994). The common name originates from their most characteristic feature—a dorsal ridge (or hump) of connective tissue in the middle of the upper back, with a small dorsal fin on the dorsal hump (Fig. 3.13). In the Indo-Pacific region, the shape and size of dorsal fin and hump, and overall body colouration vary, with large broad-based hump

Figure 3.13 Humpback dolphin mother and one year-old calf, showing conspicuous hump of the East African form *Sousa plumbea.* (Photo courtesy of L. Karczmarski.)

and grey-coloured adults in western Indian Ocean, and gently sloping ridge (no hump) and white-pinkish adults in Southeast Asia and western Pacific. In southern African waters, humpback dolphins are sexually dimorphic in length, with males larger than females (Ross *et al.*, 1994), although in Hong Kong and the South China Sea, sexual dimorphism is far less evident (Jefferson, 2000).

The taxonomic status of the genus remains unresolved. Between one and five nominal species have been proposed, but the most commonly accepted taxonomy recognizes only two species, the Indo-Pacific humpback dolphin (*S. chinensis*) and the Atlantic humpback dolphin (*Sousa teuszi*; e.g., Jefferson and Karczmarski, 2001). Taxonomic separation into three species, with humpback dolphins occurring in the western Indian Ocean referred to as *Sousa plumbea* (Indian Ocean humpback dolphin) is also used (e.g., Rice, 1998; Ross *et al.*, 1994). *S. teuszi* remains one of the least-known delphinids (e.g., Van Waerebeek *et al.*, 2004), and most of the current knowledge of humpback dolphin social systems comes from studies of the Indian Ocean *Sousa* in South Africa (Karczmarski, 1996) and west Pacific *Sousa* in Hong Kong (Jefferson, 2000).

Indo-Pacific humpback dolphins occur in shallow coastal waters, generally <20-m deep and within 1 km of shore, often near large estuaries (Ross *et al.*, 1994). In southern Africa, they are usually just outside breaking waves, <500 m from shore and 15-m deep (Karczmarski *et al.*, 2000a), in protected parts of bays or estuaries, sometimes following tidal channels into coastal lagoons (Guissamulo and Cockcroft, 2004; Karczmarski, 2000; Keith *et al.*, 2002). They display no apparent preference for clear or turbid waters, and have been seen in a variety of coastal habitats including sandy coasts, enclosed bays and coastal lagoons, mangrove channels, seagrass meadows, rocky and coral reefs and turbid estuarine waters (reviewed in Jefferson and Karczmarski, 2001; Ross *et al.*, 1994). Although in some areas they venture further offshore (up to 55 km from shore, Corkeron *et al.*, 1997; Durham, 1994; Jefferson, 2000), this happens only if the water remains shallow, and in general water depth seems to be the main physical factor limiting their offshore distribution (Karczmarski *et al.*, 2000a).

Off the Eastern Cape, South Africa, humpback dolphins are mostly seen in the morning and, to a lesser extent, in the evening (Karczmarski *et al.*, 2000b) when they forage around shallow rocky reefs (Karczmarski and Cockcroft, 1999; Karczmarski *et al.*, 2000a). These rocky reefs represent critical feeding areas for humpback dolphins within their restricted near-shore distribution (Karczmarski *et al.*, 2000a). In Algoa Bay, South Africa, dolphin activities follow a well-defined daylight pattern that varies little with seasons and tides (Karczmarski and Cockcroft, 1999), although elsewhere tidal influences on behaviour seem more noticeable (e.g., in Hong Kong, Parsons, 1998; Maputo Bay, Mozambique, A. T. Guissamulo, unpublished data).

In the Algoa Bay region, humpback dolphins forage mostly individually with little or no cooperation (Karczmarski *et al.*, 1997). However, in Maputo Bay, cooperative foraging is frequent, and often involves a coordinated chasing of schooling fish against the slopes of sandbanks and tidal channels. Further north along the Mozambique coast, in the Bazaruto Archipelago, humpback dolphins deliberately beach themselves on sandbanks while in pursuit of small fish, individually and sometimes cooperatively in small groups (Peddemors and Thompson, 1994).

In Hong Kong, humpback dolphins are restricted to the immediate vicinity of large estuaries with linear movements of only a few tens of kilometres (Hung and Jefferson, 2004). In the Pearl River Estuary, individual home range sizes vary between approximately 25 and 300 km^2, with an average of 100 km^2, which covers only part of the overall range (>1800 km^2) of a population of more than 1000 animals (Hung and Jefferson, 2004; Jefferson, 2000).

Off the South African coast, although they do not undergo large-scale migrations, movements of several tens of kilometres are common, and movements of some hundreds of kilometres are likely (Karczmarski, 1996). In the Algoa Bay region, approximately 10% of the dolphins seen in the Bay are relatively resident, but most others range widely within a narrow band along the coast (Karczmarski, 1999). Seasonal variation in occurrence, abundance and group size is considerable (Karczmarski *et al.*, 1999a) and results from seasonal immigration of humpback dolphins into, and emigration from, the Algoa Bay region in summer (Karczmarski *et al.*, 1999b). Similar summer influx of transient individuals was also seen in Maputo Bay, Mozambique (Guissamulo and Cockcroft, 2004). All studies conducted to date along the southern African coast indicate the same prevailing pattern in which some individuals are resident (possibly long-term resident), and many others display long-distance movements with ranges that might cover hundreds of kilometres of coastline (Atkins *et al.*, 2004; Guissamulo and Cockcroft, 2004; Karczmarski, 1999; Karczmarski *et al.*, 1999a,b).

Population estimates vary between 450 and 480 dolphins in the Algoa Bay region (Karczmarski *et al.*, 1999b), between about 240 and 260 at Richards Bay, KwaZulu-Natal coast of South Africa (Atkins *et al.*, 2004), and approximately 105 dolphins in Maputo Bay (Guissamulo and Cockcroft, 2004). The overall percentage of dolphins that appear to be resident is comparable between locations, although it is noticeably higher in relatively sheltered Maputo Bay than it is in the predominantly exposed Algoa Bay.

Grouping patterns of humpback dolphins seem relatively simple, with the dolphins either solitary or in small groups. In the western Indian Ocean, mean group sizes range between 6–7 dolphins in the exposed bays of the Eastern Cape coast, South Africa (Karczmarski, 1999; Karczmarski *et al.*, 1999a; Saayman and Tayler, 1979), and 15 dolphins in Maputo Bay (Guissamulo and Cockcroft, 2004). In Hong Kong, an average group contains 3–4 individuals (Jefferson, 2000; Parsons, 1998). The smallest groups are known from Moreton Bay, Australia (mean group size 2.4; Corkeron, 1990) and the Goa coast of India (mean group size 2.6; Parsons, 1998). Unusually large groups of 50–100 individuals have been seen in the Persian region, but these sightings were very unusual and it appeared that the large groupings represented aggregations of several smaller groups; generally the groups do not exceed 20 dolphins, with a mean size of 11 (Baldwin *et al.*, 2004). Nursery groups are larger and generally more cohesive than non-calf groups, at least in South African waters (Karczmarski, 1999; Saayman and Tayler, 1979), which may reflect an antipredator strategy to protect vulnerable calves. Most calves are born in summer, and gestation lasts approximately 10–12 months (Jefferson and Karczmarski, 2001). Little to no seasonal variation in group sizes occurs in Hong Kong waters (Jefferson, 2000), while in the dynamic coastal habitats of the Eastern Cape, South Africa, there are well-pronounced peaks in group sizes during summer, which corresponds with peak calving, and is probably attributed to increased inshore food abundance (Karczmarski, 1999; Karczmarski *et al.*, 1999a).

Social dynamics of humpback dolphins are fluid, with only casual and short duration affiliations. Strong bonds between individuals other than mothers and calves are uncommon, and fluid group membership represents the general pattern in both Hong Kong and South African waters (Jefferson, 2000; Karczmarski, 1999; Keith *et al.*, 2002). However, preliminary reports from Maputo Bay, Mozambique, indicate a relatively high number of stronger affiliations (Guissamulo and Cockcroft, 2004), suggesting a possibly more stable society of humpback dolphins in more protected inshore habitats of the Bay. Unfortunately, in all studies to date, the sex of only a small number of individuals was identified, which hinders more in-depth analyses of group dynamics and social structure.

An apparent temporal segregation between sexes (and possibly age classes) was seen among humpback dolphins in Algoa Bay, South Africa, and mate-searching behaviour that may involve long-distance travel was suggested to be the most likely reproductive strategy of males along the exposed Eastern Cape coastline (Karczmarski, 1999). Little evidence of alliance formation was seen in Algoa Bay, and it appeared that most fully grown males travelled either solitarily or in groups that contained both sexes. The social relationships among males might be more complex, however, and differ with habitat. Coordinated herding of a female by a group of three males and subsequent mating, similar to the pattern seen among Indo-Pacific bottlenose dolphins in Shark Bay (Connor *et al.*, 1992), was seen in Maputo Bay, although once only (A. T. Guissamulo and L. Karczmarski, unpublished data). Even though generally this behaviour seems rare, it indicates that there is likely much more diversity to humpback dolphin social strategies than currently described.

The travel range of females and their grouping pattern differ with reproductive stage, as they concentrate their activities over more restricted areas (nurseries) during lactation (Karczmarski, 1999). During that time, allomaternal grouping and care-giving behaviours are frequent (Karczmarski *et al.*, 1997), as also reported from Hong Kong (Parsons, 1998). The stretch of coast used as a nursery encompasses several feeding grounds, and its size seems to depend on resource availability (size and number of feeding grounds) and the ability of the calf to travel. As older calves better cope with difficulties of long-range movements, the stretch of coastline used as a nursery increases, and gradually the more resident female can switch to a wide-ranging pattern, until her next motherhood (Karczmarski, 1999). It is likely that male calves follow their mother's ranging and grouping pattern through adolescence, but increase their travel range at the onset of adulthood. In the generally fluid society, their interactions with other males are probably limited by competition for females, unless the distribution and availability of females is more predictable, as it seemingly is in relatively protected Maputo Bay. Otherwise, with progressing age, males may lead a more solitary and wide-ranging life, as they apparently do along the Eastern Cape coast, perhaps somewhat similar to the life pattern of male elephants (*Loxodonta africana*; Poole, 1994).

Although the current knowledge of humpback dolphin social structure is far from conclusive, and relatively little is known about their foraging behaviour and predation risk, it is apparent that for this shallow-water coastal species, their group dynamics are driven primarily by resource availability, parental needs of nursing females, and mating opportunities of males. The limited inshore resource abundance and intra-group scramble-type competition limits the group size, and the patchy distribution of foraging grounds determines the ranging pattern of the group. The demands of motherhood limit the distribution, ranging behaviour and grouping pattern of females, which in turn affect social and sexual strategies of males. The pattern of social relationships is fluid and has elements of fission–fusion, although considerably different than the classic model described earlier for large-island-associated spinner dolphins. These observations of humpback dolphin sociality fit with our predictions, with small groups of dolphins forming medium-sized communities and individuals within these communities ranging somewhat widely for available resources. There appear to be few strong bonds between individuals; however, our ability to study these dolphins is restricted by their ranging behaviour.

5.2. Killer whales (*Orcinus orca*)

The killer whale is the largest of the delphinids, with geographic variability in size and subtle aspects of colour shadings (see Fig. 3.1). It has been suggested that this disruptive colouration is useful in disorienting the killer whales' prey (i.e., a confusion effect), comprising everything from large schools of small fishes to large fishes such as salmon (*Oncorhynchus* sp.), to intermediately sized marine mammals such as pinnipeds and small odontocetes, and to the large whales such as blue (*Balaenoptera musculus*) and grey whales (*Eschrichtius robustus*). Killer whales (originally named 'whale killers' by whalers) are probably one of only a few cetaceans that have little or no predation risk, and instead have been able to refine their social systems relative to efficient hunting and the social–sexual system (Baird, 2000).

Killer whales occur in all major oceans, including Arctic and Antarctic seas, with somewhat less occurrence in much of the tropics, especially on the high seas. They usually occur in groupings of fewer than 50 individuals, although in the North Atlantic and the Antarctic, groups of hundreds appear to be common. It is not known whether such large groupings are composed of permanent schools or whether they represent temporary aggregations of several smaller units.

Most behavioural ecology (and other) research has been carried out in the US–Canadian Pacific Northwest near Vancouver Island, British Columbia (summarized by Baird, 2000; Ford *et al.*, 1998a), with other less-detailed studies off Norway (Similä, 1997), Argentina (Hoelzel, 1991) and the Crozet Islands of the southern Indian Ocean (Guinet and Bouvier, 1995). All of these studies have been of killer whales that occur within several kilometres of shore, and only recently have studies commenced on pelagic North Pacific and Bering Sea societies (Burdin *et al.*, 2001).

In the US–Canadian Pacific Northwest there are several different communities, consisting of two major types of killer whales: resident and transient. Actually, both are resident to certain areas of the nearshore, but transients tend to move faster, in straighter lines, and over greater overall day-to-day distances than residents. Residents feed largely on salmon and transients feed largely on marine mammals including pinnipeds, sea otters (*Enhydra lutris*) and cetaceans (Baird, 2000). There are three different communities of resident killer whales. The southern community consists of approximately 80 killer whales which frequent the Straits of Juan de Fuca and waters surrounding southern Vancouver Island and northern Washington (Ford *et al.*, 2000). The northern community consists of approximately 210 whales ranging from the northern parts of Vancouver Island to the Queen Charlotte Islands and southeastern Alaska (Ford *et al.*, 2000). A third community of residents, the southern Alaskan resident community, consists of at least 350 individuals which range from the Kenai Peninsula to the southern Alaska Panhandle (Matkin *et al.*, 1999a). Each of these communities is split into several different pods that frequently interact; however, rarely do individuals interact with members of different communities (Barrett-Lennard, 2000). There are also three different communities of transient killer whales; the AT1 community of 11 individuals inhabits the Prince William Sound area of Alaska (Matkin *et al.*, 1999b), the west coast transients comprise 220 individuals which range from the Alaskan Panhandle to northern California, and the Gulf of Alaska community has at least 60 members which ranges along the Pacific Alaskan coast (Ford and Ellis, 1999). Pods within each community interact, but no associations between community members have been observed (Barrett-Lennard, 2000). A third group of killer whales has been identified offshore in the Pacific Northwest, but this group has been poorly studied and little is known about its range, diet or social structure (Ford *et al.*, 2000). Community size and ranging patterns have not been investigated in detail in other areas.

Both resident and transient killer whales have the basic social unit of a matriline, consisting of one older female, her sons and daughters and the offspring of her daughters. Since killer whales live for many years, females up to 80–90 years, a matriline can consist of about four generations of maternally related whales. This is so especially for resident matrilines, which tend to be socially closed, that is, female and male offspring stay with mother throughout life. In the transient matriline, on the other hand, some offspring of both sexes may leave for long periods or life, to other matrilines or live alone, making transient matrilines smaller than those of residents, with more frequently changing association patterns (Baird, 2000). Nevertheless, transient matrilines associate with each other throughout a community, and are linked by a network of closely and more distantly related individuals that at times interact. Transient killer whales also share similar vocal calls within the community, indicating that they are learning from each other and that vocal recognition may be of importance in patterns of affiliation (Baird, 2000). The more open nature of transient society probably relates at least in part to their specializing on marine mammal prey, with fewer whales needed to take smaller animals such as sea otters or seals, and larger groupings of one dozen or more required for taking a blue whale (Tarpy, 1979) or sperm whale (Pitman *et al.*, 2001), for example. Baird and Dill (1996) showed that groups of three killer whales had the highest energy intake per whale when feeding primarily on harbour seals (*Phoca vitulina*).

In resident salmon-feeding killer whales of the Pacific Northwest, the next higher organization level from the closed matriline is the pod, made up of several such matrilines with recent maternal ancestry. Matrilines of one pod often but not always travel together. The next level is the clan, consisting of pods that share similarity of acoustic dialect. It is assumed that clans have such similarity due to ancestral splitting into related pods (Ford, 1991). The next and highest definable social level (just below that of population) is that of the entire community, consisting of pods that regularly associate with each other but never with those of another community (although, interestingly, communities may overlap; Baird, 2000).

These killer whales that have been studied to date show clear and generally long-term matriarchal societies. In resident Pacific Northwest animals this reaches an extreme with offspring staying with their mothers for life. Although actual mating has not been observed, genetic information shows that mating occurs outside their matrilines (Barrett-Lennard, 2000), probably during brief aggregations of several pods of a community. Therefore, sibling relatedness is unlikely to be more than about one-half, yet such close-knit bonds are very likely to lead to both kin and reciprocal altruism behaviour (Trivers, 1971). It is believed that such altruism, including prey sharing, is exhibited wherever killer whales have been studied (Baird, 2000).

Cooperative hunting occurs in resident and transient killer whales in the Pacific Northwest (Baird, 2000), with transients generally vocally quiet while foraging on acoustically sensitive marine mammals, and fish hunting residents usually highly loquacious (Ford *et al.*, 1998b). In fjords of Norway (Similä, 1997), killer whales coordinate swimming in tight circles, tail-slapping and bubble blasting in order to tighten herring schools, and bring them towards the surface. The basic herding techniques are quite similar to those of dusky dolphins herding anchovy schools in near-shore Argentina (Würsig and Würsig, 1980; Section 4.3). In New Zealand, killer whales at times forage on sting rays hidden beneath the sand (perhaps quite similar to feeding by Bahamian bottlenose dolphins on flatfish beneath the sand; Rossbach and Herzing, 1997), and this single-prey feeding appears to be carried out individually without apparent cooperation (Visser, 1999). In Argentina and the Crozet Islands (Guinet and Bouvier, 1995; Hoelzel, 1991, respectively), killer whales display complex strategies of taking southern elephant seals (*Mirounga leonina*) and South American sea lions (*Otaria flavescens*) near and on shore, the latter by the predators briefly beaching themselves. Often, several whales cut off potential escape routes while one whale charges the prey. Beaching appears to be a highly skilled behaviour that requires practice, and there is some evidence that adults teach young the skills that are needed (Guinet and Bouvier, 1995; Lopez and Lopez, 1985).

It is clear that killer whales have been able to develop sophisticated foraging behaviours presumably, in part, because they are relatively free from predation. This sophistication is likely enhanced by long-term social affiliations of both kin and non-kin. It is not yet clear how individuals respond within, or order themselves by sexual–activity relationships, although the highly sexually dimorphic size differences of males compared with females (Fig. 3.14) suggest that some males may obtain more matings than others do, and as such, there may be a strong tendency towards polygyny (*sensu* Kenagy and Trombulak, 1986; Lopez and Lopez, 1985). It is not known to what degree males order relationships among themselves, or indeed how much female choice is involved. It is perhaps reasonable to conjecture that in matriarchal societies of killer whales, where females and extended matrilines take care of young in a network of long-term associations, female choice of mating partners is likely to be of great importance.

Overall, killer whales particularly demonstrate food-related social organization and behaviour clearly, and which is not confounded by predation-risk effects. Killer whales that feed on salmon in the inshore waters of the Pacific Northwest occur in matriarchal societies that change little in group size (although matrilines coalesce and super-pods associate, the latter most probably for genetic exchange). Food is predictable and relatively abundant, and the whales are apparently resident to a remarkably small area even though they are apex predators. Yet matrilines are not so large as to have animals overtly competing with each other when hunting salmon schools.

Figure 3.14 Killer whale *O. orca* young adult male on the left and an immature male (or possibly mature female) on the right, off Friday Harbor, Washington State. (Photo courtesy of M. Würsig, with permission.)

On the other hand, killer whales that feed on marine mammals have a much more labile group structure, occurring from single animals to associations of 12 or more. As was mentioned previously, a group size of three appears to be most efficient for taking medium-sized seals (Baird and Dill, 1995), while it is likely that many more animals are needed to debilitate a large whale. It is also important for killer whales to keep the large whale alive while they are feeding on it, at least in deep waters, as a dead whale quickly sinks (Guinet *et al.,* 2000). When feeding on marine mammals the element of surprise is highly important, therefore mammal-eating killer whales may need to travel longer distances to encounter vulnerable prey. The exception is killer whales that feed on young pinnipeds that wander from shore rookeries; the inexperienced young prey are generally unaware of how to avoid killer whales, and the predators can station themselves at a rookery for several days to weeks at a time (Lopez and Lopez, 1985). At any rate, mammal feeders have more labile group sizes and affiliations as dictated by the need for efficiency of feeding.

The absence of predation has probably freed killer whales from the increased costs of grouping in inshore waters, unlike the costs believed to be incurred by, for example, inshore bottlenose dolphins (see Wells *et al.*, 1999a, and Section 3.1 for details). So, killer whales may be more likely to form large groups in inshore waters. It is likely that life-long association with offspring allows for highly sophisticated learned behaviours of food occurrence patterns and acquisition techniques, further encouraging the formation of larger groups. Additionally, cooperative foraging techniques probably limit competition among group members by enhancing the food resources available to the group. Beyond this, however, it may also be useful for close matrilineal kinship bonds to have animals help each other in aggregations of matrilines and ‘superpods’, during which associations it is assumed most male displays and mating take place. Killer whale males are much larger than females and show a striking dorsal fin secondary sexual characteristic. It is possible that males display to each other and/or females in order to gain access to females in oestrus, although this has yet to be confirmed directly. Matrilineal pods may be in part a bonding technique to facilitate female choice (and rejection) and confer protection from forced copulations by males.

Although cooperation can evolve among unrelated group members (Frank, 2003), the added reward of indirect reproductive success likely enhances cooperation when members of the group are related. Given the strong natal philopatry of killer whales, we would expect that cooperation with kin is a strong driving force in the evolution of killer whale social strategies, and especially in the evolution of highly cooperative foraging.

Genetics and life history information from long-finned and short-finned pilot whales (*Globicephala* sp.: Amos, 1993; Kasuya and Tai, 1993, respectively), and behavioural information on short-finned pilot whales (Heimlich-Boran, 1993), indicate that group structure and matriarchy may be quite similar to those of resident and transient killer whales in the Pacific Northwest. Pilot whale pods may be matrilineal, including apparent life-long fidelity of male offspring to the maternal pod. Pilot whales are also relatively free of predation and are sexually dimorphic. However, unlike most killer whale societies, pilot whales can occur in schools of hundreds of animals, as they move in the open ocean, feeding in large part on squid for which they need to dive to great depths. The tight matriarchal bonds in this case may strongly be linked to diving and needing to leave calves and youngsters at the surface. Thus, large group formation means individuals benefit from kin and close associates through 'babysitting' leaving mothers free to feed at depth. This system may therefore be more attuned to sperm whale societies than killer whales, per se (Whitehead, 2003). Evidence from photo-identification and behavioural observations of long-finned pilot whales from Nova Scotia, Canada, supports the sperm whale analogy, with at least some pilot whales forming long-term associations in relatively small groups (~12 individuals), while interacting briefly with many other associates (~20 individuals). However, these long-finned pilot whales do not appear to be long-term residents of a small area, but instead may be ranging fairly widely, although they return to the same general area off Nova Scotia at approximately the same time of year (Ottensmeyer and Whitehead, 2003), probably tracking food resources.

In summary, there are differences in killer whale social structure with resident (fish-eating) killer whales forming relatively large, closely related groups, foraging predominantly on individual or schooling fish. While these killer whales range much more widely than inshore bottlenose dolphins, they range less widely than some other dolphins and less than transient (marine mammal eating) killer whales that form smaller groups in order to cooperatively hunt their prey. In transients, group size is limited by competition for food within the group. Killer whales are 'freed' from serious predation and therefore resident killer whales can form larger groups than other 'resident' dolphins (see Section 3); however, competition for food limits group size in transients when they are foraging on relatively small prey items such as harbour seals. In contrast, transients form larger groups, when greater cooperation is needed to forage on large and difficult to catch prey items such as mysticete whales. Observations of killer whale sociality test the predicted framework, as predation does not exert a strong evolutionary pressure. However, it appears that even in killer whales, the availability of resources and competition for those resources are important in driving their sociality. Further revisions of this model may be required in order to fully apply it to communities with strong matrilineal bonds as have been observed in killer whales and suggested in pilot whales.

5.3. Comparisons with terrestrial mammals

It is inherently difficult to make generalizations about the intermediate classification pattern, as it falls somewhere on the continuum between local and wide-ranging communities. However, some generalizations can be made. It is probable that many delphinid species fit into this intermediate pattern, although few have been investigated in sufficient detail due to the difficulties in studying animals that live in small- to mid-sized groups and range over fairly wide areas of sea. While humpback dolphins have been studied in a number of areas (see Section 5.1), these studies represent relatively short-term snapshots of a specific area and understandably therefore do not give a very complete picture of their lives. We speculate that humpback dolphins live in a world of moderately predictable resources, with some site fidelity, but mostly over a much larger area than the inshore resident dolphins. They display fluid associations with other individuals, and the need to keep moving to find food probably limits long-term contact with other individuals and strong bonding. Predation pressure is not sufficiently high to cause large groups to form, and in fact individuals probably reduce predation pressure more by refuging in complex habitats or surf zones when they are available. Food resources are not always available, nor are they entirely clustered in relatively rare but superabundant patches. Therefore, solitary individuals or smaller groups are often most effective for locating food, while at the same time reducing competition. Additionally, if different individuals have different goals (e.g., immediate need for food, protection of young or mating), then this will increase the fluidity of associations as groups fission commonly and regroup with different membership. This pattern is likely to prevent the formation of long-term complex bonds.

The resource dispersion hypothesis (RDH) suggests that when resources are patchy but reasonably abundant, the costs of group living may be reduced and groups form even if there are no direct benefits to the individuals (Johnson *et al.*, 2002). Typically, when resources become more abundant, individuals should reduce their territory (or home range) to reduce travel and territorial maintenance costs. However, if resources are not evenly distributed (in space or time), then a reduced home range may not contain all of the required resources. Instead, it would be beneficial for an individual to maintain a larger home range that encompasses sufficient resources, even if at times this range could support more individuals. Thus in habitats with patchy but rich resources, competition between individuals may be reduced and individual ranges may support additional animals in the range at relatively little cost to the primary animals (Johnson *et al.*, 2002). This model may be relevant to describe the evolution of sociality in several carnivore species, especially those that do not cooperate extensively within these groups. There have been numerous difficulties in testing this model, many of which relate to accurate measures of territory size as well as resource dispersion and availability (Johnson *et al.*, 2001).

Humpback dolphins and other 'intermediate' ranging dolphins are clustered in groups that do not appear to be generally cooperative and they exploit resources that are heterogeneously distributed. The RDH may well describe the sociality of these dolphins; however, it remains to be tested.

The evolution of cooperative and altruistic behaviours in killer whales has led to a very different pattern of sociality than observed in humpback dolphins. Among cooperative terrestrial animals, individuals in larger groups appear to have higher reproductive success as larger groups are better able to cooperate (e.g., meerkats, *Suricata suricatta*; Clutton-Brock *et al.*, 1999). Thus there is selection for larger groups in highly cooperative animals. Pilot and killer whale group sizes mostly support this suggestion, as they tend to be found in larger groups than more resident or other intermediate-ranging dolphins (compare Sections 3 and 5.1 with 5.2). However, scramble-type competition for food resources may limit group size (see Baird and Dill, 1996). Group size may be maintained by the eviction of subordinate individuals (as observed for meerkats; Stephens *et al.*, 2005) and suggested in transient killer whales (Baird and Whitehead, 2000). Further investigation of the similarities and differences between cooperative terrestrial mammals and killer whale sociality may yield important insights.

While there are clear differences between killer whale and elephant societies, there are many similarities. As in killer whales, adult elephants face little predation pressure and form a multi-tiered social structure consisting of matrilines that will associate with other related matrilines (Wittemyer *et al.*, 2005). While elephants feed on a wide variety of plants, their large body size and low digestive efficiency means that they require very large quantities of food to sustain themselves. Therefore, they range fairly widely to find food, and resource competition limits group size. Family units consist of related females and their dependent young. These units remain together throughout the year (dry and wet season), indicating that these groups may be the largest that can be supported by the environment without leading to resource competition. New family units appear to form after the death of the matriarch, when the matriarch's surviving daughters split into separate family units. These new family units will frequently merge (especially during the wet season when food resources are more abundant); however, such associations are relatively brief (Wittemyer *et al.*, 2005). A similar pattern is seen in killer whales with family-based units, which frequently associate with close kin and less frequently associate with more distantly related groups (Baird, 2000).

Among delphinids, the killer whale pattern of sociality may relatively be rare and driven in large part by extensive cooperative behaviour between kin. Thus far it appears restricted to the subfamily Globicephalinae, which includes the pilot and killer whales as well as false and pygmy killer whales (*Feresa attenuata*) as well as the melon-headed whale (*Peponocephala electra*). Unfortunately, relatively little is known about the social structure of the melon-headed whale as well as false and pygmy killer whales.

6. DEMOGRAPHIC, SOCIAL AND CULTURAL INFLUENCES

Societies tend to some stability in space and time. A one- or even five-year description of a group of bottlenose dolphins in a bay system, for example, shows births, deaths, variations in affiliations, but no large-scale change in habitat use or social structure. It is not until societies are studied for longer that we observe either slow changes or the occasional rapid wholescale invasion of new habitat (e.g., bottlenose dolphins abruptly moving north off the California coast; Wells *et al.*, 1990), disappearance from an area (e.g., pilot whales disappearing from the Catalina Island area; Shane, 1995), or large variation in community size and structure (Wells *et al.*, 1999a). It has generally been assumed for dolphins that such changes are due to extrinsic environmental factors, but studies of chimpanzee societies show that much community structure and habitat use can be ascribed to behavioural interactions, or 'internal politics' of individual associations in the community (Wrangham and Peterson, 1996).

In the light of chimpanzee and similar studies on land, it appears worthwhile for us to re-examine the causes of subtle long-term and abrupt changes in habitat use and social affiliations in delphinids. For example, pilot whales were known to feed off the southern California Channel Islands in the late 1970s and early 1980s, but in 1982 abruptly disappeared, with Risso's dolphins frequenting the pilot whales' former areas (Shane, 1995). The most likely explanation for the distributional change is the effects of ecological factors, such as the apparent concomitant decline of nearshore market squid (*Loligo* sp.) upon which pilot whales feed. However, we simply do not know whether intrinsic (to the community) social factors might have been at least partially responsible, such as one community converging with the Channel Island one, and other alternative travel and habits being adopted by the latter. Competitive exclusion between Risso's dolphins and pilot whales could be another factor. There is evidence for rapid community-wide adoption of a new behavioural pattern (a particular male song display) in humpback whales (*Megaptera novaengliae*; Noad *et al.*, 2000), but this has not been clearly demonstrated in delphinids. One of us (Karczmarski *et al.*, 2005) recently showed that two communities of Hawaiian spinner dolphins converged at Midway Island, with an abrupt habitat shift by one that had apparently been resident in an atoll elsewhere. The shift was possibly caused by ecological factors, but also possibly by group splitting due to increasing group size in one community, competitive exclusion by others elsewhere, or any number of social interaction factors. While the habitat shift was abrupt, there was a well-documented slower, greater than one year, gradual acceptance by the resident community of the newcomers. We can presently only speculate as to the resultant social changes of affiliation, mating and calf rearing. It is to be hoped that present and future studies of such special cases like this will help describe the complexity of ecological and social interactions responsible for demographic and societal change.

It is probable that much of the observed stability in space and time is due to animals occupying habitat that fulfils their requirements, and the likelihood that adjacent habitats are already occupied by conspecifics or others using resources there. Continued use of the same habitat likely results in individuals adapting to it and an increased chance of adopting behaviour patterns best suited to the habitat. Such behavioural specificity, as observed in sympatric communities of killer whales that feed either on fish or marine mammals (summarized by Baird, 2000), is probably perpetuated by transmission of information within a generation ('horizontal' transfer, among similar-age peers) and from generation to generation ('vertical' transfer from mothers and 'oblique' from older non-relatives) by, in a broad sense, culture (Rendell and Whitehead, 2001). Once different cultures are established, it becomes unlikely that animals of one culture adopt that of another one, even though some gene flow may be occurring between them. It is also possible that cultural differences allow sympatric communities to coexist without, or with only muted, competitive exclusion. Lack of competition would depend on amount of overlap of required spatial resources for foraging, rest away from predators and inclement weather, for example. Furthermore, it is possible in delphinids with differing culturally transmitted ways of living, that 'gene-cultural hitch-hiking' (when selection favours individuals that share a culturally transmitted behaviour simultaneously selects the genes these individuals possess, without the genes possessing any inherent benefit) may result in a somewhat different genetic make-up of communities or populations (as indicated by Laland, 1992, and suggested for cetaceans by Whitehead, 1998).

7. COMPARISONS WITH OTHER CETACEANS

While delphinids comprise the most diverse group of cetaceans, several other families exist and the social structure of some of these species has been studied in some detail. We suspect that many of the same forces influencing delphinid social structure also operated on the evolution of other odontocete social strategies. Only the porpoises (family Phocoenidae) and the four different families of river dolphins (family Platanistidae, Iniidae, Lipotidae and Pontoporiidae) are similar in size or smaller than most of the dolphins. It is likely that predation pressure strongly influences the social structuring of these taxa, although there may be relatively few predators for some of the river dolphin species. In contrast, the beaked whales (family Ziphiidae), sperm whales (family Physeteridae and Kogiidae) as well as the beluga (*Delphinapterus leucas*) and narwhal (*Monodon monoceros*; family

Monodontidae) are larger than most of the Delphinidae. Thus, many of these species may be less vulnerable to predation from sharks (Jefferson *et al.*, 1991; Heithaus, 2001b) especially as adults, although killer whales are capable of killing even adult sperm whales (Pitman *et al.*, 2001).

7.1. Sperm whales (*Physeter macrocephalus*)

Sperm whales are the largest of the odontocetes and have one of the most complex social strategies described so far. They are also one of the most sexually dimorphic species with mature females rarely longer than 11 m, while mature males may be longer than 18 m. Sperm whales are found throughout the world's oceans, usually in waters deeper than 1000 m. Females and their young are typically in equatorial and subtropical waters, rarely ranging higher than 40° North or South. Mature males tend to forage at high latitudes, often near the ice edge, although they will migrate to equatorial waters to breed. Sperm whales feed opportunistically on a wide variety of squid in the deep-scattering layer, routinely diving 400–600 m. The social structure of sperm whales has been best studied in the Eastern Tropical Pacific, focusing on sperm whales identified near the Galapagos and the west coast of South America (see review in Whitehead, 2003).

Female groups appear to range over large areas (on the order of 1000 km), although they remain in these large areas for long periods, on the order of decades. Longer range movements have been recorded, in particular many females appear to have left the Galapagos area for example, and have been re-identified along the west coast of Central and South America, from the Gulf of California to northern Chile (Whitehead, 2003). On a daily basis, females can move quickly over large areas or remain in a small area for hours to days, although the average mean displacement (straight line distance) was 70 km d^{-1} (Whitehead, 2003).

Adult sperm whales are probably not vulnerable to predation by sharks, and may be much less vulnerable to killer whale attacks than the smaller delphinids; however, adult sperm whales have been successfully hunted by killer whales (Pitman *et al.*, 2001). Calves do appear to be particularly vulnerable to predation, especially as young calves do not seem to be capable of diving to the mother's foraging depths (300–800 m) or for the time required to successfully forage (dive times average 40 min; Gordon, 1987; Papastavrou *et al.*, 1989). Whitehead (1996) outlines how this vulnerability of calves may have driven the evolution of sperm whale social structure.

Calves remain with their mothers until approximately age 6 when males begin to emigrate from their natal group. As the males mature, they cluster in progressively smaller groups consisting of other subadult males, and they forage at increasingly higher latitudes. By the time the males are sexually mature (approximately age 20) they tend to be solitary and forage in Arctic and Antarctic waters, often near the ice edge. Around age 25, males begin to migrate to equatorial waters where female groups are located. These large, sexually and socially mature males tend to avoid each other, and rove between groups of females, spending relatively short periods (hours to days) with each group, presumably mating with all receptive females in the group. Genetic paternity testing indicates that some males father more than one offspring in a group, likely indicating that at least two females were receptive during the male's brief visit. After mating, a mature male will leave the group, presumably to attempt to locate another female group or return to high latitude feeding grounds (Whitehead, 2003, and references therein).

Male–male competition for access to female groups appears to be based on size or vocalizations (which may be an honest signal of male size), although conflicts do also occur (Whitehead, 2003). The sexually based distribution of sperm whales has probably evolved through the requirement of males for increased food resources to achieve and support their larger body size. Thus, sexual selection for large body size in males may have restricted the development of large groups composed of mature adults of both species.

Females lead a more complex, stable social existence. Female offspring remain with their mothers past sexual maturation, forming long-term bonds with 8–12 other females, which are often but not always kin. These 'units' (following the terminology of Whitehead, 2003) remain together for a long time; recorded associations persist over 10 years, although units can on occasion merge, split or individuals transfer between units. Units routinely join to form a 'group', an association that typically lasts 1 to 2 weeks. In fact, sperm whales are most often encountered in a group composed of 20–24 females and dependent males. Often there is not a mature male present, but if there is it is typically only one male (Whitehead, 2003).

When there are no young calves present in the group, all group members tend to surface and dive synchronously, such that whales are present at the surface for approximately 8–10 min, followed by about 40 min with no whales at the surface. However when a young calf is present, the group members tend to dive asynchronously, such that at least one adult-sized individual remains at the surface at all times, and the calf appears to associate with a number of different individuals, over the course of its mother's foraging dive. The evolution of babysitting behaviour can be explained through kin selection (as most of the females have some maternal kin present in the group) or through reciprocal altruism, where babysitting services may be returned at some later time, or a combination of the two factors (Whitehead, 1996).

The presence of an adult-sized babysitter likely provides increased vigilance to detect a predator, and may deter attacks by sharks. Killer whales will attack sperm whale groups, and it appears that the adults will cooperate to defend the young by forming a protective circle around the young.

In addition to providing babysitting, it has been suggested that individual females will nurse not only their own calves but also the calves of other females (Whitehead, 2003).

Therefore, a female's need to reduce the risk of predation of her calf may have selected for the formation of long-term bonds between females, especially between kin to provide babysitting services. Females may also be able to limit competition for food resources by specializing on rich, patchily distributed squid, and by spreading out and forming foraging ranks to increase detection rates of these rare, but abundant patches. However, sperm whales' large body size and subsequent energetic demands may restrict groups to much smaller sizes than seen in Eastern Tropical Pacific dolphins (Section 4.1). Competition for food resources may play an important role in the temporary fission and fusion of units into groups, and in the relatively rare, but important cases of unit membership change.

Sperm whale social structure seems to fit the pattern described for wide-ranging delphinid communities (Section 4). However, competition may limit group size, and increase the formation of bisexual groups. Additionally, female cooperation appears to be an important aspect in protecting offspring from predation and may have lead to the formation of long-term bonds, and a predominantly matriarchal society. There are additional levels of grouping and social complexity observed in sperm whales, including acoustically based clan groups similar to killer whales (Section 5.2), which are beyond the scope of this chapter on delphinid social structure (see Whitehead, 2003, and references therein for more detail).

7.2. Northern bottlenose whales (*Hyperoodon ampullatus*)

Northern bottlenose whales are a relatively large beaked whale (7–9 m in length); approximately the same size as male killer whales. They are found only in the North Atlantic, typically in deep water (>1000 m) from Nova Scotia, Canada (44°N) to Scotland, with a potentially disparate concentration near the Azores. Northern bottlenose whales have a specialized diet, focusing mainly on squid from the genus *Gonatus*. They are deep divers, routinely diving deeper than 800 m. Little is known about predation risk faced by bottlenose whales. Few individuals bear scars easily identifiable as unsuccessful shark or killer whale attacks. Their large body size likely means that bottlenose whale adults are relatively safe from shark predation; however, calves are probably still vulnerable and all ages are likely to be vulnerable to killer whale predation. Their biology and social structure has been studied in detail in the 'Gully', a submarine canyon located offshore of Nova Scotia, Canada (Gowans, 2002) and which serves as a useful example for comparison with the principal features of delphinid social groups.

This submarine canyon and the surrounding area (~100 km along the shelf break) support a resident population of 160 (Whitehead and Wimmer, 2005). Given that the whales are present in relatively large numbers, it is presumed food is predictably available in the canyon, and given that the whales concentrate in the Gully, and to a lesser extent in other smaller canyons in the area, that the canyons represent a locally higher concentration of resources. The social structure of northern bottlenose whales resembles that of inshore bottlenose dolphins (Section 3.1). Northern bottlenose whales are typically found in small groups (average 3, rarely more than 10 individuals), females appear to have no preferential associates, while mature males form long-term bonds (Gowans *et al.*, 2001). Nursery groups were not clearly identified, perhaps because young calves were only occasionally sighted and there was no clear evidence of babysitting. Little is known about the diving abilities of young bottlenose whales, although young animals were not observed at the surface for longer periods than adults (Gowans, 1999). Males were not observed herding or attempting to sequester females, nor has mating behaviour been observed. Male–male competition was observed once, with two males (who had in previous years been long-term associates) head-butting each other in several bouts. Shortly after the head-butting behaviour, one of the participating males was observed in association with a sexually mature female (Gowans and Rendell, 1999). This suggests that male–male bonds are probably not the only route to male reproductive success which is similar to observations of bottlenose dolphins in Shark Bay, Australia (Krützen *et al.*, 2004).

The social structure of northern bottlenose whales, at least in the Gully, resembles the pattern described for resident bottlenose dolphin communities (Section 3). Competition for the limited food resources available in the canyon may limit group sizes and the overall community size. Predation is either not a strong enough force to lead to the formation of large groups or the need to reduce food competition prohibits routine formation of large groups. Within this resident community, males may be able to sequester females, leading to the formation of long-term bonds between males to increase access for females. It is not clear, however, if the observations in the Gully are generally applicable to all northern bottlenose whale communities, or if this community's reliance on a reliable food source in the submarine canyon has led to the evolution of a relatively unique social structure.

7.3. Harbour porpoise (*Phocoena phocoena*)

Harbour porpoises are smaller than most delphinids (1.5–1.7 m). They are found along the coastlines of the North Atlantic and North Pacific, as well as in the Black Sea. Their small size means that they are vulnerable to predation by a number of species of sharks as well as killer whales. They typically feed individually on benthic fish. The social structure of harbour porpoises has not been studied in detail, largely because they are mostly solitary. While small groups (two to five) individuals are observed, the species is generally considered asocial (Bjørge and Tolley, 2002). Harbour porpoises may predominantly follow a refuging from predators' strategy, remaining in relatively complex inshore and coastal habitats and avoiding groups as a way to reduce predator detection (similar to forest-dwelling oribi; Brashares and Arcese, 2002; Section 3.3). The relative asociality of harbour porpoises and several other members of the porpoise family may indicate that predation risk on very small species may be too great to lead to the formation of groups. However, a paucity of studies means this question has yet to be investigated fully.

7.4. Why are there no long-term bonds in baleen whales?

Baleen whales (Sub-order Mysticeti) adopted a different style of living from that of predatory odontocetes due to the formers' capability of batch feeding quite low on the trophic level. This resulted in a concomitant increase in mouth and body size, large energy reserves, and therefore seasonal feeding together with the capacity for migrations away from feeding areas for safe mating/calving. Migratory mysticetes do not seem to have the long-term and complicated social bonds that appear normal among delphinids. Instead, they loosely affiliate on the feeding grounds with only short-term bonds, such as tandem-feeding in blue whales (Schoenherr, 1988), bubble-netting in humpback whales (summarized by Clapham, 2000), and echelon-feeding bowhead whales (*Balaena mysticetus*; Würsig *et al.*, 1985). In general, they do not need to coordinate foraging strategies to take large swarms of mysids or stands of ampeliscids (grey whales), euphausiid crustaceans (blue and fin whales; *Balaenoptera physalus*), and fishes and squid (the majority of balaenopterids). Their size also makes them relatively free of predation as adults, with the notable exception of occasional encounters with large groups of killer whales (Tarpy, 1979). Therefore, there is no need for the coordinated (perhaps, cooperative) social matrix of familiarity for feeding, migration or predator avoidance. However, humpback whales in Chatham Strait, Alaska, routinely forage cooperatively to form bubble nets to encircle schooling herring. Instead of only forming brief associtions to cooperatively build bubble nets (as observed in most other areas; Clapham, 2000), 22 of these humpback whales formed a core group which routinely cooperatively foraged together, displaying associations that lasted over subsequent years (Sharpe, 2001). Individuals within this group tended to take on certain specific roles (e.g., bubble blower, vocalizer), suggesting that when individuals routinely cooperatively forage, formation of long-term bonds and task specializion may be important, even among mysticetes.

Migrating mysticetes meet on the mating/calving grounds and seasonal affiliations, displays of dominance among males (apparently in large part mediated by sound) and some variable gregariousness among females (right whales *Eubalaena glacialis*; Payne, 1995) do exist. Although social/sexual systems have been inadequately described, it is unlikely that tight bonds of affiliation exist, at least beyond one season. There are no matriarchal or other long-term associations beyond the mother–calf bond that lasts for one year or slightly less, depending on species.

Non-migratory mysticetes, such as some populations of minke (*Balaenoptera acutorostrata*; Dorsey, 1983; Dorsey *et al.*, 1990), Bryde's (*B. brydei*) and pygmy right whales (*Caperea marginata*), may more closely resemble some odontocete social groupings, with longer term small group affiliations, but research to substantiate or refute this possibility has simply not been carried out. The non-migrating mysticetes are generally the smaller of this suborder, tend to feed throughout the year, feed in a less individual batch style than do the larger species, and have much to gain from being in association with others, such as for food and predator avoidance. This area is ripe for dedicated research, and we look forward to comparisons with smaller mysticetes and some delphinid societies. However, we make this observation in advance of such studies: odontocetes are macropredators with tight social strategies interwoven with large behavioural flexibility and large brains. Mysticetes might be thought of as being in line with the ungulate model of behavioural strategy, with certainly impressive behavioural capabilities, but little evolution of sophisticated foraging and therefore social strategies.

8. Conservation Implications

As highlighted in previous sections of this chapter, social systems are not fixed features of species but often show intraspecific variations that are a result of individual attempts to maximize fitness under local environmental circumstances. Collectively, these studies indicate that as environments vary in the conditions and resources they provide, so do delphinid social systems. As social systems frequently place constraints on which individuals are able to breed, and thereby determine the reproductive success of individuals and effective population sizes, understanding how environmental variation affects social structure is of major concern in conservation management (Durant, 1988; Komdeur and Deerenberg, 1997; Parker and Waite, 1997; Pettifor *et al.*, 2000). Therefore, it is important to consider the incorporation of social structure into predictive models of populations (where changes in certain parameters suggest changes in management approach; Pettifor *et al.*, 2000) and population viability analyses (Durant, 2000). This is particularly so when a predictive model is used to explore the effects of management perturbations, because these may influence the population indirectly through their effects on social structure, as well as directly through their effects on survival or fecundity (Pettifor *et al.*, 2000), as was the case with elephants in Lake Manyara National Park, Tanzania (Prins *et al.*, 1994).

The effective size of populations, the most sensitive predictor of the ability of any populations to maintain genetic variability and persist through time, is greatly affected by the breeding sex ratio, and social and mating systems of animals (Parker and Waite, 1997). Understanding of animal social strategies and reliable modelling of the distribution of reproductive success are key components for understanding population dynamics. For the needs of predictive conservation modelling, behavioural description of social systems may be sufficient to characterize the mating system, even if the underlying genetic structure is difficult to investigate, as is often the case in studies of delphinids.

In everyday management practice, it is important to know what aspects of a population determine its vulnerability. However, it is through understanding the behaviour of individuals that we can understand populations, and predict their potential trajectories in response to demographic changes or anthropogenic impacts. A number of recent studies, both terrestrial and marine, have incorporated social structure into population viability analyses of small mammalian populations (e.g., Martien *et al.*, 1999; Vucetich *et al.*, 1997; Young and Isbell, 1994). These models consider such factors as social grouping, territoriality and the effective availability of mates, providing a framework by which key elements of social structure can be incorporated into essentially demographic models (Pettifor *et al.*, 2000), and facilitate better management practices. However, in most cases these models do not assume individual behavioural strategies to change in response to changing conditions, which becomes a problem when predicting responses of large and/or wide-ranging populations. For some land mammals, where the flexibility of social systems is better understood, sensitivity analyses have been conducted allowing 'what if' scenarios to be explored. As a result, management strategies have been developed to manipulate these systems by varying the environmental determinants of the variation (Komdeur and Deerenberg, 1997; Pettifor *et al.*, 2000). A better understanding of delphinid social system might have similar application in future management considerations, especially during the design and management planning of coastal Marine Protected Areas.

Studies of sperm whales in the Eastern Tropical Pacific highlight the crucial importance of social strategies to effective conservation. Stock structures of marine species have been very difficult to determine, especially in highly mobile species such as sperm whales. When stock structures were incorporated into management plans, they were often defined more on easy-to-identify geographic boundaries rather than on knowledge of how the animals were distributed. Sperm whaling in the 1960s and 1970s off the coast of Chile targeted mature males and ended (at least in part) when whales could no longer be profitably encountered. This pattern of sex-biased whaling may have led to the elimination of most of the mature males that could potentially migrate to the Galapagos to breed with females. In fact, Whitehead *et al.* (1997) found very few mature male sperm whales in the Galapagos in the 1980s and 1990s, and also found very few young calves. While some males were being born into the population, the prolonged delayed sexual and social maturity in sperm whales and sexual segregation of males meant that there was a 25–35 year lag between the birth of a male and his presence back on the mating grounds to potentially father offspring (see Section 7.1 for more details). Survival of a sufficient number of mature males through the period of intense whaling in the 1960s and 1970s may relate to a potential for improved birth rate and recovery from whaling in the present.

9. CONCLUDING COMMENTS

In conclusion, our predictive framework fits well with most of the observed patterns of delphinid sociality. Small communities of dolphins tend to remain resident in small ranges. These dolphins form labile networks of associates and male bonds sometimes form in order to gain access to females. Observations suggest that these dolphins tend to forage individually on relatively solitary prey, and reduce their predation risk by hiding from predators or avoiding risky areas of their habitat (Section 3). In contrast, large groups of dolphins tend to form in coastal areas and the open ocean where grouping may be the only strategy to reduce predation risk. Membership in these large groups may change over time, with most individuals forming only brief associations. These dolphins range widely and may cooperatively forage for rare but abundant prey such as large schools of fish (Section 4).

While these observations lend support for the framework proposed here, no tests of this framework have been conducted to date. In fact few studies on delphinid social structure have included testable predictions to support or disprove a suggested hypothesis. Additionally, this chapter highlights the many gaps in our understanding of dolphin behaviour, especially our understanding of foraging behaviour and predation risk. However by establishing a predictive framework that attempts to explain the observed social strategies, we can now design studies that will test these predictions. Alterations to this model will likely be made in the future (or perhaps a new model will be needed); however, great advances in studying the evolution of sociality in the terrestrial environment were made once predictive frameworks were established (such as Jarman, 1974; Wrangham, 1980).

It is also clear in this chapter that although studies have begun to elucidate many of the details of delphinid social strategy, important questions remain. The potential complexities of these systems are vast and varied. Further research into the social strategies of relatively unstudied species may provide valuable tests of the concept underlying the framework outlined in this chapter. Variations in social strategies among different individuals and different communities will also test this framework. It is likely that the conceptual framework we propose is an oversimplification of the multitude of different forces acting on dolphin social strategies. However, we hope that it may serve as a starting point to test some of these theories, and it may be especially valuable as a way to compare different communities of the same species as well as between different species.

There is an inherent bias against studying wide-ranging open ocean species of dolphins, as it is simply more costly and difficult to locate and follow them. Current advances in remote sensing make it possible to track the movements of large marine animals using satellite-linked tags which transmit information about an individual's location, behaviour and physiology as well as features of its environment (Ropert-Coudert and Wilson, 2005). As these electronic tags become smaller, easier to attach and less expensive, it may be possible to sample a large number of individual dolphins from a single pod and ascertain whether they remain together for long periods. Additionally, we may be able to measure when these individuals are feeding, and on what. If a large number of predators are also tagged, then we will gain valuable insight into the predation risk faced by dolphins. Passive acoustic monitoring will also become a more valuable technique for examining details of dolphin distribution and movements. By conducting large-scale, multifaceted research projects that incorporate ocean ecology as well as cetacean sociality, we will gain valuable insight into the remarkable lives of delphinids.

Cetaceans have clearly diverged from terrestrial mammals in the 55-plus million years since a group of ungulates adopted a predominantly aquatic lifestyle (Gingerich, 1998; Thewissen, 1998). However, it is clear that they maintain many mammalian characteristics that have exerted different evolutionary forces than fish and other marine organisms face. Thus delphinids share many similarities with other mammals, despite their marine lifestyle. Above all, we need to view dolphins and other odontocete cetaceans as large brained social predators (similar to carnivores) that face challenging predation risks (similar to ungulates) and complex social strategies and relationships between individuals (similar to primates). By doing so, our understanding of dolphin social strategies may approach that of some terrestrial mammals including humans.

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