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Chapter 5
The Significance of Marine Mammal Predation on Salmon and Sea Trout

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Abstract: There is evidence that stocks of Atlantic salmon (Salmo salar) are declining on both sides of the Atlantic. There is also concern over the health of sea trout (Salmo trutta) populations, particularly on the west coast of Scotland. The decline in salmon abundance appears to be related to a decrease in marine survival. This decline, together with a concurrent growth of some marine mammal populations, has led to an increased interest in the impacts of marine mammals on salmonids. We review the published information on predation by marine mammals on salmon and sea trout. There is no evidence that marine mammals are the main causal agents for the decline in salmonid abundance. However, in areas where salmonid abundance is already low, they could have substantial local effects on populations. Problems in assessing, and defining, significant predation are discussed. Although to assess the significance of marine mammal predation fully it must be put in an ecosystem context, we are some way from achieving this.

Introduction

Atlantic salmon and marine mammals may be bracketed together as charismatic megafauna, which tend to have special value in the minds of many people. Moreover, these animals support local sporting and tourist industries and each group is a focus for conservation plans in many parts of their ranges. The possibility that marine mammals may seriously adversely affect populations of salmon and sea trout is therefore particularly concerning and potentially difficult to manage.

There is an evident need for good information on the importance of predation by marine mammals on Atlantic salmon and sea trout in the sense of how much damage occurs and what the consequences are for the prey populations and the fisheries. This issue has been notoriously difficult to address, in large part for two main reasons. First, the population biomass of salmonids is limited by the extent of their freshwater rearing habitat with the consequence that, overall, they are rare animals at sea, although they may occur at high densities locally. It has often been calculated that even if the population of grey or harp seals consumed the entire population of Atlantic salmon, they would be rare items in the diet. Extrapolating from measure-
ments of rare diet items to estimate the consumption of a prey species by a population is inevitably associated with very high levels of uncertainty. Second, the technical problems involved in studying the diets of marine mammals are formidable. This issue is a recurring theme throughout this chapter, which concludes on the optimistic note that new methods might soon be available to help improve estimates of the impacts of some species of marine mammal.

The chapter is arranged as a series of topics. The first section describes, in broad terms, some of the types of interactions between fisheries and marine mammals. A brief outline is then provided of the aspects of population dynamics that are particularly important to consider when evaluating impacts of predators on prey. A section then summarizes the biology of the prey and is followed by an account of the available data on consumption of Atlantic salmon and sea trout by marine mammals. Finally, the issue of assessing the significance of impacts is considered and the chapter is concluded with a brief discussion.

**Interactions between marine mammals and fisheries**

Most species of marine mammal interact with fisheries (Northridge & Hofman, 1999). Such interactions are often classified as operational or biological. Operational interactions occur when the marine mammal becomes directly involved with fishing operations, for example, the by-catch of dolphins in the east tropical Pacific tuna fishery (Beverton, 1985; Gosliner, 1999). Biological interactions tend to be more complex, and their effects on prey densities are less obvious, than those resulting from operational interactions (Northridge & Hofman, 1999). One type of biological interaction occurs when there is competition between marine mammals and man over commercially exploited fish stocks, such as Atlantic salmon (Beverton, 1985).

Biological interactions may have beneficial or detrimental effects on the marine mammal and the fishery (Northridge & Hofman, 1999). Considering effects of fisheries on mammals, it has been suggested that industrial fisheries in the North Sea have reduced sand eel stocks producing negative impacts on predatory fish, sea birds and seals (Naylor et al., 2000). However, it is also possible that declines in the stocks of predatory fish, possibly due to fishing, have allowed sand eel, and hence seal and sea bird, populations to increase (Northridge & Hofman, 1999; Furness, 2002). Predators have the potential to deplete fisheries seriously as indicated by the estimate that Californian sea lions (Zalophus californianus) were consuming more than half of the threatened steelhead trout (Oncorhynchus mykiss) returning to the Lake Washington watershed (Fraker, unpublished observations). Fishermen often view marine mammals as competitors, and historically their hostility towards seals in the UK has been due in part to the perceived effect they may have on the Atlantic salmon population (Harwood & Greenwood, 1985; Woodward, 2002).
Some principles of predator–prey interactions

Understanding the interactions of predators and prey is key to the study of ecology (Begon et al., 1996). Predators and prey affect each other in a variety of different ways and over wide ranges of spatial and temporal scales. On an evolutionary timescale, predation can produce both morphological and behavioural adaptations in predator and prey species (Krebs & Davies, 1993; Skelton, 1993). Prey tend to evolve ever-increasing abilities to avoid predators, while predators tend to evolve increased efficiency at capturing prey. The impacts of particular predators on their prey may depend on an extent on where they are in this evolutionary arms race and how important the prey are in the predators’ overall diet.

Predation is one of the key mechanisms underpinning population and community dynamics (Matson & Hunter, 1992). Consequences of predation can be pronounced and some predators can produce ‘top down’ control of some ecosystems by regulation of their prey populations (Pace et al., 1999). In most cases, the role of marine mammals in shaping communities is unclear (Bowen, 1997). However, it has been suggested that the presence of harbour seals (Phoca vitulina) in Lower Seal Lake, Quebec, has drastically modified the fish community, particularly the population of lake trout (Salvelinus namaycush) (Power & Gregoire, 1978), although this work did not account for other potential causal agents.

Salmon and sea trout are subject to predation throughout their life cycles, from a wide variety of different predators (e.g. Mather, 1998). However, the impact of predation probably varies with life stage. Self-thinning is thought to occur in the early stages of freshwater development in some populations of salmonid, implying that an increase in the mean weight of individuals (i.e. growth) can occur only through a reduction in density by emigration or death (Grant & Kramer, 1990; Elliott, 1993; Grant, 1993; Armstrong, 1997). This natural removal of individuals may provide a surplus that can be harvested by predators without them having an effect on the eventual population size (compensatory mortality). It is even possible that predation could have a positive effect by thinning populations of stunted prey to speed the growth of the survivors to a size at which they can reproduce and contribute to harvest. There is little evidence for density-dependent mortality (and hence compensation) beyond the early parr stage, although it may occur in some situations (Armstrong, 1997). It has been considered unlikely that Salmo spp. would be affected by density-dependent mortality in the marine environment where they occur at comparatively low densities (Crozier & Kennedy, 1993; Hansen, 1993). Predation on salmonids from the smolt stage onwards may therefore result in a proportional reduction in the number of adults returning to spawn.

The effect of predation on prey populations depends in part on the relationship between the densities of predators and their prey. It has long been recognized that there are two major components to the population dynamics of predators and prey. The functional response is the relationship between the number of prey eaten per predator and prey density (Solomon, 1949). The numerical response is the relationship between
the predator density and prey density (Solomon, 1949). A numerical response can occur through changes in predator density due to mortality and reproduction (reproductive response) and immigration and emigration of predators (aggregative response) (Readshaw, 1973). It is important to consider these responses when assessing impacts of predators. For example, regarding the functional response, a prey species may be ignored when it is at low density, but at higher densities a predator may switch to feed almost exclusively on it. At the higher prey densities, the predators may aggregate in the area where the prey species occurs, in a numerical response.

Salmon and sea trout

The genus *Salmo* contains two species, Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*), both of which are commercially important (Crisp, 2000). Atlantic salmon occur on both sides of the Atlantic Ocean and follow an anadromous life history during which many of them leave fresh water to feed in the marine environment before returning to spawn (Crisp, 2000). However, in many populations, a large proportion of the males spawn before migrating to sea, whereas substantial female maturation in fresh water is restricted to a few populations in North America. Populations of brown trout, which is originally a European species, exhibit both resident (entirely freshwater) and anadromous forms of both sexes. The anadromous form of *Salmo trutta* is commonly known as sea trout. Due to human introductions, trout are now distributed around the world (Elliott, 1994).

Although the life histories of both salmon and trout are remarkably plastic, they share a common underlying pattern of development (Crisp, 2000) (Table 5.1). The timing of the various life stages can produce differences in life strategies, denoted by nomenclature. For example, a salmon may spend only one winter at sea and return to the river as a grilse (one-sea-winter fish) or it may stay in the sea for more than one winter (multi-sea-winter fish) and is then known as a salmon (Mills, 1989). Similarly,

<table>
<thead>
<tr>
<th>Stage</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alevin</td>
<td>Hatched fish still dependent on the yolk sac for nutrition.</td>
</tr>
<tr>
<td>Fry</td>
<td>Short transitional stage where the fish emerge from the redd and start to feed and disperse.</td>
</tr>
<tr>
<td>Parr</td>
<td>Stage between full absorption of the yolk sac and smoltification or maturity.</td>
</tr>
<tr>
<td>Smolt</td>
<td>Stage when seaward migration occurs.</td>
</tr>
<tr>
<td>Post-smolt</td>
<td>Stage from departure from the river (usually in spring) to the end of the first winter in the sea.</td>
</tr>
<tr>
<td>Adult</td>
<td>Mature fish which return to the place of their birth to spawn.</td>
</tr>
<tr>
<td>Kelt</td>
<td>Adult fish which has lost condition due to spawning.</td>
</tr>
</tbody>
</table>

Table 5.1 Stages in the life cycles of Atlantic salmon and trout. Italics are used to indicate life stages that occur in sea trout and salmon but not brown trout. [Adapted from Mills (1989) and Elliott (1994).]
finnock or whitling are brown trout that migrate to sea and return to fresh water within the same year, whereas sea trout are those that return in different years (Elliot, 1994). These details of the life history are important, because the impact of marine predation on the population depends on how the sea-going fraction of the population interacts with those that remain in fresh water. Furthermore, the ratio of grilse to multi-sea-winter fish may affect the impact of predation depending on where it occurs. If losses are mainly in coastal areas, then salmon experience two periods of high vulnerability, irrespective of time spent at sea, as they leave and return to rivers. However, if predation occurs in the open sea, then multi-sea-winter salmon are most vulnerable because of the overall time they spend in the marine environment. The timing of return to fresh water may also be important because the burst swimming speed of fish depends on the water temperature (which varies seasonally), while that of the warm-blooded seals is more constant. Hence, early-running spring fish may be particularly susceptible to predation in the coastal region.

After entering the marine environment, salmon undertake long migrations to reach their feeding grounds (e.g. Mills, 1989; Reddin & Short, 1991; Hansen, 1993; Shelton et al., 1997; Reddin & Friedland, 1999). For example, salmon in the Faeroes area have been shown to originate from Norway, Sweden, Iceland, Canada, Russia, Scotland, Ireland and Spain (Hansen & Jacobsen, 2000; Jacobsen et al., 2001). Lengths of migration among sea trout are highly variable; some fish travel as much as 600 km, whereas ‘slob trout’ never leave the estuary (Berg & Berg, 1987; Crisp, 2000). It appears, however, that most sea trout stay in coastal areas, relatively close (within 80 km) to their natal river (Pratten & Shearer, 1983; Berg & Berg, 1987). An estuary may contain a mixture of sea trout from neighbouring rivers (Pratten & Shearer, 1983).

There is evidence that catches of Atlantic salmon, and hence stocks, are in decline on both sides of the Atlantic (Hawkins, 2000) and sea trout are declining on the west coast of Scotland (MacLean & Walker, 2002). The decline in abundance of salmon appears to be caused by a decrease in marine survival. The cause of this decline has been the subject of conjecture and may relate to variations in ocean climate, perhaps through growth-mediated predation (Friedland et al., 2000; Hawkins, 2000).

**Marine mammal predators of salmonids**

The species for which we have found documentary evidence of predation on Atlantic salmon at the post-smolt and marine adult stages are listed in Table 5.2. In the following section we summarize the published information on five of the known marine mammal predators of salmonids in the Atlantic Ocean. These are selected merely on the basis that they have been the subjects of most study.

**Grey seal (Halichoerus grypus)**

Grey seals are found throughout the north Atlantic and form three distinct populations: north-west Atlantic, north-east Atlantic and Baltic (Macdonald, 2001). Male
grey seals are larger than females; for example, NE Atlantic population females reach 180 cm in length (150 kg) and males 200 cm (200 kg) (Anderson, 1990).

Grey seals are primarily benthic foragers and take a wide variety of prey species (e.g. Thompson et al., 1991; Bowen et al., 1993; Bowen & Harrison, 1994; Hammond et al., 1994; Goulet et al., 2001). Although they are largely pelagic, salmonids have been reported to occur in the diets of grey seals on both sides of the Atlantic (e.g. Pierce et al., 1989; Hammill & Stenson, 2000). Of the 361 grey seal stomachs examined in Scotland between 1958 and 1971 that contained prey items, 97 (27%) contained salmonids (Rae, 1960, 1968, 1973). More recent work based on faecal analysis has failed to find evidence of salmonids in the diets of UK grey seals (e.g. Hammond et al., 1994; Thompson et al., 1996). It has been suggested that salmonid otoliths (the ear bones used to identify many types of prey) are not represented in seal faeces because they are fragile (Boyle et al., 1990) and because of the possibility that seals may not consume the heads of large prey (Pitcher, 1980). It is known that heads are discarded when salmon are available to seals at unusually high densities, for example, in salmon nets and at salmon farms. However, seals are capable of consuming the heads of large fish and there is little or no evidence that heads are discarded routinely in the wild. Preliminary studies have also revealed no tendency for captive seals to discard salmon heads irrespective of prey availability (Middlemas, unpublished observations). The discrepancy between the previous estimates of diet might be explained by the fact that many of the seals in the early studies originated from near salmon nets on the east coast of Scotland (Pierce et al., 1991). This is an important consideration; there seems to be no doubt that seals can use nets as traps and/or as ambush points to catch substantial numbers of salmon. The difficulty in drawing meaningful comparisons between studies is further compounded by the fact that the diet of grey seals is known to vary by area, season and year (e.g. Bowen et al., 1993; Hammond et al., 1994; Mohn & Bowen, 1996).

Some individual grey seals have been observed consuming salmon in rivers, but generally they use rivers less often than harbour seals (e.g. Anderson, 1990; Carter et al., 2001) even though they are the more numerous of the two species in the UK (Anon., 2001).
Harbour seal (Phoca vitulina)

Although known as the common seal in the UK, in the rest of the world *Phoca vitulina* is known as the harbour seal, after its habit of frequenting sheltered waters (Anderson, 1990). Of the five recognized subspecies, three occur within the Atlantic. *P. vitulina vitulina* occurs in coastal areas of the eastern north Atlantic, *P. v. concolor* is found around the coasts of the western north Atlantic and *P. v. mullonae* is resident in freshwater lakes and rivers in the Hudson Bay area of Canada (Rice, 1998). *P. v. vitulina* and *P. v. concolor* and the Pacific harbour seal, *P. v. richardii*, are known to enter rivers and lakes (e.g. Smith et al., 1996; Rice, 1998; Yurk & Trites, 2000; Carter et al., 2001). Harbour seals have been observed consuming salmonids (*Salmo* spp. and *Onchorhynchus* spp.) in fresh water (e.g. Brown & Mate, 1983; Roffe & Mate, 1984; Carter et al., 2001; Yurk & Trites, 2000).

Salmonids have rarely been reported in the diet of *P. v. concolor* (e.g. Selzer et al., 1986; Bowen & Harrison, 1996). In contrast, they have been found in numerous studies of *P. v. vitulina* diet. Of the 117 harbour seal stomachs collected in Scotland between 1956 and 1971 that contained prey items, 21 (18%) contained salmonids (Rae, 1960, 1968, 1973). Subsequent studies have used analyses of faecal samples and have tended to find less evidence of salmonids (Pierce et al., 1990, 1991). For example, annually salmonids occurred in 0–2.86% of the faecal samples collected during the summer in the Inverness Firth (Tollit, 1996). Based on a comparison of the digestive tracts of seals shot near salmon nets and elsewhere, Pierce et al. (1991) concluded that between-study differences in diet may reflect variation in the abundance of different prey.

Detailed observations of the behaviour of harbour seals have been undertaken within the estuaries of the Rivers Don and Dee in the UK (Carter et al., 2001). Seals were observed to consume a variety of fish species, and the minimum number of adult salmonids consumed within the study area was estimated to be an order of magnitude lower than the rod catch. The presence of seals in the rivers was highly seasonal, and appeared to be related to the breeding and moulting behaviour of the seals rather than the abundance of salmonids (Carter et al., 2001). Numbers of seals associated with rivers have been shown to be correlated with numbers of Atlantic salmon smolts leaving the River Lussa, Scotland, (Greenstreet et al., 1993) and the return of adult chum salmon (*Oncorhynchus keta*) to Netarts Bay, Oregon (Brown & Mate, 1983). Caution should be applied to interpretation of such results. For example, Greenstreet et al. (1993) suggested that the increase in the abundance of seals at the mouth of the Lussa may have been related to an increase in marine productivity rather than a response to the increase in smolt numbers.

Harp seal (Phoca groenlandica)

This species is named after the harp-shaped markings on the backs of the mature animals (Macdonald, 2001). They weigh up to 130 kg, grow to a length of 170 cm and live for up to 30 years. Harp seals are found in three breeding populations: north-east
Newfoundland and the Gulf of St. Lawrence, the east coast of Greenland and around Jan Mayen Island, and in the White Sea off the coast of Russia. They are most widespread outwith the breeding season when they are dispersed throughout the north Atlantic. The total population size is estimated to be approximately 7 million (Macdonald, 2001) and there is evidence that the north-west Atlantic population is increasing (Stenson et al., 2002). Analyses of stomach contents have shown that salmon are rare or absent in the diets of harp seals (e.g. Lydersen et al., 1991; Beck et al., 1993; Lawson et al., 1995; Lindstrom et al., 1998; Wathne et al., 2000).

To date, studies have suggested that salmon is either rare (harp and grey) or absent (harbour and hooded) from the diets of seals in Atlantic Canada. Even so, the consumption by seals in 1996 was estimated to be possibly in the order of 3300 tons (Hammill & Stenson, 2000). The majority of this consumption was by harp seals.

Harbour porpoise (Phocoena phocoena)

Harbour porpoises inhabit shallow coastal waters in temperate north Atlantic, north Pacific, Baltic and Black Seas (Rice, 1998; Macdonald, 2001). They are small cetaceans that grow to 140–200 cm and weigh 40–80 kg (Macdonald, 2001).

Predation by porpoise was once thought to have a large controlling influence on the abundance of Atlantic salmon in the Baltic (Svärdsön, 1955). However, analysis of their diet and habitat use led Lindroth (1962) to reject this hypothesis. Similarly, there is little evidence of salmon occurring in the diets of harbour porpoises in the Atlantic (e.g. Rae, 1965; Recchia & Read, 1989). Salmonid remains were found in only a single porpoise out of a sample of 138 animals from the Gulf of St. Lawrence (Fontaine et al., 1994). The species of salmonid could not be determined from its remains.

Bottlenose dolphin (Tursiops truncatus)

Bottlenose dolphins are found in the coastal waters of most tropical, subtropical and temperate regions (Reynolds et al., 2000; Macdonald, 2001). Individuals found in warmer tropical regions tend to be smaller than those found in cooler temperate locations and males in the UK can grow up to 410 cm in length (Thompson & Wilson, 1994).

Information on the diet of bottlenose dolphins in UK waters comes from analysis of stomachs of stranded animals. Remains of salmon were present in two of eight dolphins stranded within the Moray Firth region of Scotland, including one animal found entangled in a salmon net (Santos et al., 2001). It is not possible to extrapolate these figures meaningfully to a population or species level due to the small number of dolphins examined (Santos et al., 2001).

Bottlenose dolphins in the Moray Firth are often seen consuming large salmonids (Wilson et al., 1997; Janik, 2000) (Fig. 5.1). It has been suggested that temporal and spatial patterns of habitat use exhibited by dolphins in this area may be linked to the migration of salmonids (Wilson et al., 1997; Hastie, 2000). It has also been suggested
that these dolphins may use specific vocalizations to manipulate the behaviour of salmon to make them easier to catch (Janik, 2000).

Assessing the significance of predation

Modelling and experimentation can be used to estimate the impact of marine mammals on salmonid stocks. Experimentation would involve the manipulation of marine mammal numbers by removal or addition and the monitoring of subsequent changes in the population of fish. This approach has a number of drawbacks. For example, there are logistic and political difficulties associated with the manipulation of numbers of marine mammals; it is difficult or impossible to achieve the necessary replication; natural fluctuations in salmon mortality caused by other factors may mask any effect of predation; due to the long life cycle of salmonids the experiment may have to run for many years; and it is difficult to devise suitable controls. In some circumstances it may be possible to use natural changes in predator populations, such as an increase in mortality caused by disease, in place of experimental manipulations. In the absence of direct experimental data, modelling may be considered to be a useful tool for developing further understanding of the impacts of marine mammal predators. We suggest that there are four key questions that need to be addressed in
order to assess fully the significance of marine mammal predation on stocks of salmonids.

**Does the predator eat salmon and sea trout?**

Information on the diet of animals can be obtained through direct observations of feeding and this method has been used to study seal predation on salmonids (Roffe & Mate, 1984; Carter et al., 2001). However, this technique is dependent on the availability of sufficient numbers of suitable observation points. Information obtained is limited to the area of observation and biased to large prey items consumed at the water surface (Roffe & Mate, 1984). Indirect methods used to study diet include the use of stable isotopes, fatty acids and the analysis of prey remains found in stomachs or faecal material (e.g. Pierce et al., 1991; Hammond et al., 1994; Hooker et al., 2001).

As mentioned in the previous section, salmonids have been documented in the diets of a number of marine mammals (Table 5.2). It is possible that other species may consume salmonids. For example, although we did not find evidence of killer whales eating salmonids in the Atlantic, they are known to eat Pacific salmon (*Oncorhynchus* spp.) (e.g. Saultis et al., 2000), and would be unlikely to select against Atlantic salmon.

**How much of each life stage of salmon and sea trout does the predator consume?**

There are several approaches to estimating the amount of salmonids consumed by predators, one of which is the use of bioenergetic models (e.g. Mohn & Bowen, 1996; Hammill & Stenson, 2000; Boyd, 2002). It is possible to use this type of model to incorporate changes in energy requirements associated with season and the ages and sexes of the individuals within populations (Mohn & Bowen, 1996; Boyd, 2002). Using such a bioenergetics model, Hammill & Stenson (2000) estimated that during 1996, grey and harp seals consumed 3229 tonnes of Atlantic salmon. However, it is difficult to evaluate this figure without further information on the stock size and other causes of mortality.

The impact of predation will partly depend on the numbers and the life stages of salmonids consumed. Each individual smolt has a lower chance of contributing to a rod fishery or spawning stock than a returning adult does and this factor has to be taken into account when comparing predation on different life stages. For example, a predator could consume 2.5 kg of food as a 2.5-kg adult or 100 25-g smolts. If each smolt had a 10% chance of returning to the river, then the impact of predation on the smolts would be greatest, as ten of these would have returned as adults had they not been removed.

The consequences of consumption of kelts are difficult to assess. In many systems, kelts have a low chance of returning to spawn again. But does this mean that losses to predators are of little relevance, or are losses to predators the reason for the low return rate? The answer to this question is not known.
How does consumption of salmonids compare with stock sizes and other causes of mortality?

Estimates of consumption can be used to give an impression of the likely extent of interactions between predators and prey (e.g. Hammond, et al., 1994; Brown et al., 2001). For example, the consumption of salmonids by a small number of seals in the mouths of the Rivers Don and Dee in northern Scotland was estimated to be an order of magnitude less than the rod-and-line catch (Carter et al., 2001). In this instance, the impact of seal predation on the salmonid stocks is likely to be small, although disturbance caused by seals entering fishing boats may have a larger impact on the fishery. It is possible, however, that proportionately greater damage occurs during some specific months of the year, for example during spring, when salmon are most highly valued as sport fish. Carter et al., (2001) did not analyse their data by season, presumably because of inadequate sample sizes.

How would changes in the level of predation affect the prey population?

A problem with modelling impact is that usually the populations of predator and prey and the diet of the predator are sampled at one or few points in time. Both the numbers and the proportion of the prey population consumed by each predator are likely to vary depending on the densities of predator and prey. Therefore, models may have very limited value for predicting impacts of predators. As previously mentioned, predators can respond to changes in the abundance of prey species through numerical and functional responses. Molin & Bowen (1996) compared estimates of grey seal predation on cod assuming two different types of functional response. The proportion of cod in the diet was constant in one model but increased with the availability of cod in the environment in the other model. The estimated consumption of cod was considerably larger when they were assumed to comprise a constant fraction of the seal diet. Therefore, predicting the future consumption of cod depends on the assumptions made regarding the responses of seals to changes in cod abundance. A numerical response may be important when salmon become aggregated at high densities due to a year of high abundance or local conditions, such as drought, impairing up-river migration. Any factor that tends to delay salmon in areas where they are particularly vulnerable to predation is likely to increase the prey death rate. It is probably important that salmon move quickly through coastal waters where they are aggregated and may be most vulnerable to ambush from seals and dolphins.

It is often felt that a reduction in predator numbers will result in an increase in prey abundance, and thereafter fisheries catch. Figure 5.2 illustrates this scenario as a food web (Beverton, 1985). Although seemingly counter-intuitive, it appears that under certain circumstances predation may be beneficial to a fishery. An example of this effect is the interaction between the fishery for deep-water hake (Merluccius paradoxus) and the Cape fur seal (Arctocephalus pusillus pusillus) in the Benguela ecosystem in South Africa (Fig. 5.3). In this system, fur seals may be beneficial to the
Fig. 5.2 Graphical representation of a simple food web linking a fishery and predator of a single prey species. Direction of arrow indicates the flow of energy from the prey species to the fishery and predator (Beverton, 1985).

Fig. 5.3 Food web characterizing the interaction between Cape fur seals and the hake fishery in the Benguela ecosystem (Punt & Butterworth, 1995; Yodzis, 2001).

Fishery because they consume the shallow-water hake (*Merluccius capensis*) which consumes juvenile deep-water hake (Punt & Butterworth, 1995).

A more complicated situation arises when the marine mammal consumes both a predator of the target species and the target species itself. An example of such a situation may occur in Rogue River, Oregon, where harbour seals are known to consume steelhead (*Oncorhynchus mykiss*) and Pacific lamprey (*Lampetra tridentatus*) (Fig. 5.4; Roffe & Mate, 1984; Beverton, 1985). Any changes in seal predation will have consequences for both the steelhead and the lamprey. If seal numbers decreased...
in the short term there should be a subsequent rise in the abundance of steelhead. However, in the longer term there will also be an increase in the lamprey population, which may well result in a decrease in the abundance of steelhead. Depending on the strengths of the interactions involved, the net result of predation by marine mammals may be either beneficial or detrimental to the fishery (Beverton, 1985; Yodzis, 2001).

Such theoretical models are useful in highlighting the highly variable, and occasionally counter-intuitive, effects marine mammals may have on prey populations. A complete food web covering the whole life cycle of salmon and sea trout would necessarily need to be highly complex (Yodzis, 2001). Further complications arise from the need to model interactions explicitly within a spatial and ontogenic framework (Hollowed et al., 2000). For example, because of the density-dependent factors discussed earlier, compensation for predation may vary depending on when and where it occurs.

It is not always necessary to model explicitly every component of an ecosystem to gain insights into predator–fisheries interactions (Bax, 1998; Yodzis, 1998; Livingston & Jurado-Molina, 2000; Hilton et al., 2001; Yodzis, 2001). For example, Bjorge et al. (2002) explored the interactions of harbour seals and fisheries using a combination of energetic and spatial modelling. They were able to identify areas of potential conflict and suggest both negative and positive effects of predation on fisheries.

Discussion

Predators may be considered to have an adverse impact if they cause a reduction in the value of fisheries or affect the conservation status of stocks by reducing the densities of spawning fish below those needed to saturate systems with eggs and maintain genetic diversity. At present there appear to be no cases documented in the scientific literature of marine mammals having been shown to have a large impact on stocks of Atlantic salmon or sea trout, except at farms and netting stations, although there is good evidence that they damage stocks. There have been no large-scale experiments to estimate impacts of marine mammals, and in most cases the second of the four key questions is still being addressed: how much does the predator consume?

Research into the diet and behaviour of seals has resulted in some useful insights into the application of science for managing interactions between marine mammals and salmon. There is clear evidence that some individual seals enter rivers and consume salmon. However, it also appears that damage caused by a few such salmon specialists is low compared to the rod catch (Carter et al., 2001). Simple energy balance equations readily demonstrate that individual seals specializing on adult grilse can potentially remove only small components of the stocks from east coast Scottish fisheries (Middlemas et al., unpublished). However, seals near smaller rivers and where salmonid numbers are low could have larger impacts on stocks. There may be other costs that are more difficult to quantify. In particular, little is known about the impact of seals on smolt runs, and the presence of seals in pools in rivers is widely
anecdotally reported to have a negative impact on the chances of anglers catching salmon. Certainly, the presence of seals may deter anglers from a fishery.

Targeted removal, for example by scaring, is likely to have maximum benefit, per animal removed, if it is directed at individual ‘salmon-specialist’ seals. However, it should be considered whether the costs in time, money and public relations balance what may be rather limited benefits. The cost–benefit analysis may vary depending on whether the damage is primarily from consumption of adult salmon near the estuary or reduction in the catchability of fish further up the river. It is important that it is clearly established whether there are distinct individual seals that specialize in feeding within rivers or a larger sector of the population that uses rivers more occasionally. Furthermore, it is important to establish how rapidly removed specialist river seals (should they exist) are replaced by other individuals.

The remainder of the seal population (non-salmon-specialists), because of their large number, could have a high impact on the salmon stock if they occasionally took salmon at levels that have been too low to detect or quantify. In cases where seals haul-out near rivers, existing methodology using faecal analysis may give an indication of the likely scale of impact (Middlemas et al., unpublished). However, in other cases, new techniques are required to detect traces of salmon in the flesh of marine mammal predators. Analysis of fatty acids may offer some improvement in the scope for identifying the past diets of seals and other mammals, but it is not clear whether rare dietary items, such as salmonids, could be differentiated from common prey.

Major technical problems with faecal analyses include the uncertainty about the proportion of occasions when heads of salmon are discarded by predators and the difficulty of differentiating salmon and sea trout from their otoliths. It is possible that these problems can be circumvented if assays can be developed to identify and distinguish between the DNA of salmon and sea trout in seal faeces.

Marine mammals have the potential to cause serious damage to populations of Atlantic salmon and sea trout. There is direct evidence of local impacts, particularly from harbour seals and bottlenose dolphins, in areas where salmon aggregate near river mouths and in rivers. However, in very few cases have attempts been made, or has it been possible, to quantify the magnitude of these impacts. The estimation of broader-scale impacts has been seriously hampered by the rarity of salmon remains in the diets of marine mammals and the low numbers of samples available.

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References


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