

## CHAPTER 17

**ECOSYSTEM MONITORING: ARE SEALS A POTENTIAL TOOL FOR MONITORING CHANGE IN MARINE SYSTEMS?**

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**INTRODUCTION**

Marine ecosystems are vast and complex biological networks, which are dynamic in structure at a range of spatial and temporal scales (Nicol *et al.* 2000). The dynamic activity of these systems is driven ultimately by variation in climatic conditions, some of which are cyclic, such as El Niño-Southern Oscillation (ENSO) events (Jaksic 1998) and the Antarctic Circumpolar Wave (ACW) (White and Peterson 1996). Variation in climatic conditions has important repercussions for the location and abundance of primary production (i.e. phytoplankton), which in turn contributes the distribution and abundance of secondary producers (grazers) and ultimately, top predators (those vertebrates that feed on species within the upper levels of the oceanic food webs such as fish, crustaceans and cephalopods) (El-Sayed 1988; Sullivan *et al.* 1993; Abbott and Barksdale 1995; Priddle *et al.* 1998).

The last 150 years has seen increasing levels of anthropogenic influence superimposed on these pre-existing natural environmental fluctuations through increased fishing activity (Furness and Tasker 2000) or global climate change (Banks *et al.* 2000). However, the extent and impact of these new influences is often difficult to detect at the level of primary or secondary production, due to practical difficulties in monitoring large areas of

ocean for sufficient periods of time. Given this, several authors have suggested that the performance of top predators that are reliant on the dynamics of lower trophic levels, may be used to provide insight into some aspects of the lower trophic levels (Wanless *et al.* 1982; Rindorf *et al.* 2000; Thompson and Ollason 2001). Here, the assumption is that elements of the behaviour, reproductive output and health of top predators should reflect the availability and quality of food in the marine environment.

However, there are many problems that must be addressed before any top predators may be used as monitors of anthropogenic change. For example, even if indices of predator performance can be demonstrated to reflect prey abundance or availability, there may be a mismatch between foraging areas and areas where prey stock assessments for commercial fisheries are required. Furthermore, prey abundance and predator performance are unlikely to be related linearly, potentially making predator indices a poor guide to prey abundance. For example, predators may be able to compensate for declining prey abundance by increasing some aspect of their foraging effort that is not readily detectable from shore-based studies (e.g. Harcourt *et al.* 2001). Alternatively, the predators may switch to another prey species and maintain their overall energy intake. These

types of problems may be overcome, but the relationship between the predator and their prey needs to be well understood before monitoring can reveal meaningful trends and relationships. This may also require a large number of variables to be monitored simultaneously.

For the purpose of this review we will concentrate on trophic processes. Other types of human-induced environmental change, such as marine pollutants, are addressed in Chapter 21 (this volume). In the broadest sense, there are two types of questions that may lend themselves to monitoring at the ecosystem level. These are long-term environmental fluctuations due to climate change (such as global warming or ozone depletion) and the potential effects of commercial fishing. However, both of these processes operate on a variety of temporal and spatial scales, and not all top predators are equally suited to monitoring all ecosystem processes.

Our overarching objective is to examine natural systems as a model to detect a range of marine predator responses to human-induced changes in the environment. Therefore, we first review and critically assess the applicability of using pinnipeds as potential monitors of environmental variability by examining the link between the 'performance' of seals in relation to natural fluctuations in the marine environment. This will establish if it is possible to measure whether seals respond to existing environmental variation with currently available technology. If they do not, then they are unlikely to serve as monitors of potentially subtler, human-induced change. We also discuss the type of demographic and behavioural responses that seals exhibit, and examine these at a range of temporal and spatial scales. We then discuss specific studies that have attempted to use seals as 'bio-indicators' of environmental variation. We pose the question: were these studies successful in their aims, and if not, what were the reasons for their failure? Based on our examination of previous studies, we discuss which species would be most suitable as monitors and what biological measures could potentially yield the most useful information regarding changes in the marine environment. Finally, we comment on the magnitude of anthropogenic change these approaches could detect, and the problems associated with concurrent nature and human-induced changes in the environment.

#### **PINNIPED RESPONSES TO NATURAL ENVIRONMENTAL VARIABILITY**

In this section we assess whether it is possible to measure the effects of natural environmental variability on seal physiology, behaviour and reproductive success. The biological effects of environmental variation can appear in several aspects of seal life history, and these may operate at specific spatial and temporal scales of investigation. Where possible, we have separated the specific influence of spatial and temporal variability on life-his-

tory measurements; however, the nature of environmental variability is complex. Spatial and temporal effects are often intertwined, occasionally making it impractical to adhere to this approach.

For example, surrogate measures of marine productivity, either satellite images of primary productivity (i.e. chlorophyll *a* concentration as measured by sea surface colour variation), or by ship-based measures of prey species (e.g. krill, fish or cephalopods) may be correlated to predator performance at completely different spatial scales. These scales depend both on the distribution of the prey aggregations in time and space, as well as on the foraging capacity (i.e. swimming performance) of the predator and the resolution of the technology used to track them. For instance, while Hunt *et al.* (1992) found that the relationship between Antarctic fur seal (*Arctocephalus gazella*) distribution and krill distribution peaked at a 52 x 52 km grid size, Jaquet *et al.* (1996) found that the relationship between chlorophyll *a* concentrations and sperm whale (*Physeter macrocephalus*) distribution was best at spatial scales of ~900 x 900 km grid size.

#### **Foraging parameters**

As foraging is by necessity linked to the distribution and abundance of prey, variation in diet, feeding behaviour and foraging locations have the potential to be indices of changes in prey.

#### **Diet**

Only a few studies have examined temporal changes in diet for a particular pinniped species, some of which found annual variation in diet composition (e.g. Read 1990). However, others have not (Härkönen 1987; Hall *et al.* 1998). The breadth of diet of many pinnipeds may limit the power to detect annual differences except when profound changes occur. Sample sizes are invariably limited and subtle differences, such as a change to a younger age class of the same prey species, while indicative of a fundamental change in prey composition, may be undetectable using current methods of dietary analysis. Consequently, it has been suggested that behavioural parameters such as diving and foraging behaviour may sometimes be more sensitive to changes in the abundance and distribution of prey resources (Bengtson 1988).

Several studies have described differences in diet between geographically distinct populations of the same species, which may indicate regional differences at the ecosystem level such as prey community composition. Studies of Antarctic fur seals at various populations in the southern ocean have shown that diet varies markedly between krill- (*Euphausia superba*) based ecosystems (e.g. Bonner 1968; Doidge and Croxall 1985; Reid 1995; Reid and Arnould 1996) and non-krill-based systems (e.g. Green *et al.* 1997; Klages and Bester 1998; Lea *et al.* 2002). Similarly, Green and Burton (1987) attributed differences in cephalopod biomass in Weddell seal (*Leptonychotes weddellii*) diet to

ecosystem differences. Caution is required when interpreting comparative data because changes in diet among colonies may also be attributable to differences in predator breeding status, age and sex composition (Gales *et al.* 1993).

### Foraging location

Shifts in local abundance and availability of prey resources could be affected by variance in biological and physical features in the ecosystem (Bengtson 1988). For example, Sydeman and Allen (1999) found that the offshore abundance of harbor seals (*Phoca vitulina*) was higher during years of higher sea surface temperatures, which may reflect the seals' inability to find sufficient prey in coastal waters under these conditions. Antarctic fur seals have been shown to concentrate foraging in areas of colder oceanic water (Boyd *et al.* 2001), and lactating subantarctic fur seals (*A. tropicalis*) breeding on Amsterdam Island tend to forage in oceanic areas of 14–16°C, in the northern part of the Subtropical Front (Georges *et al.* 2000). Like Gentry and Kooyman (1986) and Costa (1993) before them, Georges *et al.* (2000) suggested that top predators such as fur seals require food resources to be sustained by highly productive and seasonably predictable oceanographic features.

As well as variance in geographic location, seals may use space differentially in the vertical plane. Deep-diving pinnipeds, like southern elephant seals (*Mirounga leonina*), sometimes appear to link their foraging behaviour to the physical properties of the water column, such as temperature (Boyd and Arnborn 1991; Campagna *et al.* 2000; Field *et al.* 2001). It is not yet known whether this is because the seals use temperature as a physical cue to the presence of prey, or if their prey congregate at the thermic discontinuities between water masses.

### Foraging behaviour

Foraging trip duration and the number of trips made by female otariid seals are regarded as sensitive measures of annual differences in prey availability. Bengtson (1988) found that Antarctic fur seal foraging patterns over 20 years, as inferred from layering in teeth, indicated clear periodicity in the mean number of feeding trips. This phenomenon appeared to reflect the abundance of local prey within the foraging range of this species.

Duck (1990) found for Antarctic fur seals that accumulated mass, foraging trip duration, and pup mortality differed between years in response to lower food availability in one of three years; however, daily energy expenditure did not change either because females were unable, or unwilling, to work harder (Costa *et al.* 1989). At the same colony, Boyd *et al.* (1994) found differences in dive behaviour, in particular dive bout type, in years of contrasting prey abundance. This contrasts with the findings of Costa and Gentry (1986) for northern fur seals (*Callorhinus ursinus*), where metabolic rates differed between years, but not foraging trip length, or body mass. Antarctic fur seals

may therefore be operating nearer to their metabolic maximum when foraging (Costa *et al.* 1989), when compared to northern fur seals.

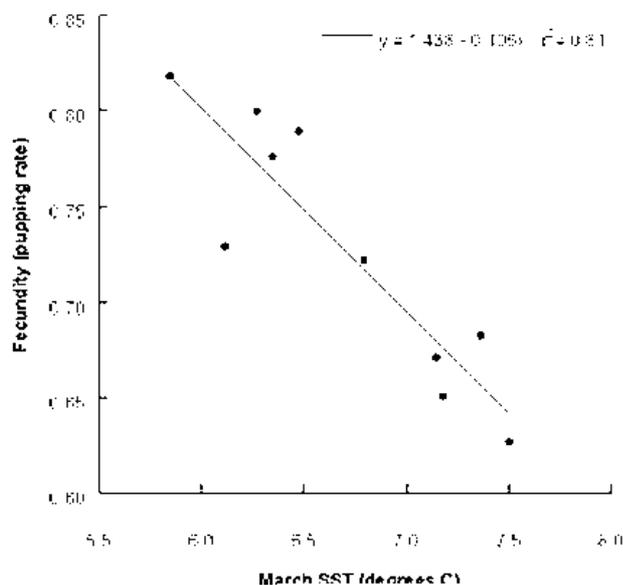
Neither Georges *et al.* (2000) for subantarctic fur seals, nor Harcourt *et al.* (2001) for New Zealand fur seals (*A. forsteri*), found consistent differences in diving behaviour among years. For the latter study, it appears that the lack of differences were a function of the low power to detect differences in generalist predators capable of opportunistic feeding and prey switching (Harcourt *et al.* 2001). Therefore, behavioural shifts among years of contrasting prey abundance are more likely to be detectable in specialist predators.

### Breeding parameters

Although foraging parameters are linked directly to prey availability, the previous section has indicated that there are considerable inter-species differences in how well these can be detected. Characteristics of the breeding performance of pinnipeds, however, may provide an integrated summary of prey availability. The timing of reproduction in Antarctic fur seals appears to be determined, in part, by environmental factors such as climate patterns (Duck 1990). There is a greater synchrony in arrival of females compared to males, making the former more amenable to the detection of differences among years (Duck 1990). Females arrived later in years following a period of lower availability of resources and had lower rates of pup production (Duck 1990). Inter-annual differences in reproductive rates for South American fur seals (*A. australis*) from harvested animals (proportion of pregnant females) have been found by Lima and Páez (1995), although no connection to environmental variation was demonstrated.

Growth rates of pups do, however, show clear inter-annual differences. Georges and Guinet (2000) detected annual (two years) differences in post-natal growth rates in subantarctic fur seals and Read (1990) showed that body condition of mother and calf harbour porpoises varied over three years. These changes were related to changes in the proportion of the main diet item consumed. Bradshaw *et al.* (2000) found that body condition in New Zealand fur seal pups varied relative to the predicted food availability resulting from normal ENSO oscillation. As well, Trillmich (1986) reported an increase in yearling weights and female haul-out duration during 'good' years, and Doidge *et al.* (1984) reported that annual variation in pup growth rates were greater than differences observed between two sites of differing population density.

Doidge *et al.* (1986) also found some significant regional differences in female Antarctic fur seal attendance patterns among different sites ( $n = 3$ ) and years (3–4). However, Testa (1990) found no significant differences in reproductive rate or age at first reproduction after correcting for sampling bias (timing,



**Figure 1** The relationship between fecundity, defined as the proportion of females known to be alive giving birth in a particular year, and sea surface temperature recorded within the foraging ranges of the seals the previous March. The data are from *A. gazella*, from Macquarie Island (Goldsworthy, unpublished data).

intensity) among Weddell seal populations at three disparate sites. Here, there was also some regional replication of annual periodicity in reproductive parameters measured (Testa 1990).

Cyclic patterns in pinniped reproductive rates (Testa 1987, 1990; Burton 1998), foraging patterns (Bengtson 1988), age structure (Laws 1984) and vagrant haul-out patterns (Rounsevell and Eberhard 1980) have been found in many species of high-latitude pinnipeds (e.g. Weddell, crabeater (*Lobodon carcinophaga*) and leopard (*Hydrurga leptonyx*) seals, Antarctic fur seals). It has been suggested that these cyclic patterns are related to periodic environmental patterns such as ENSO (Testa 1990; Testa *et al.* 1991) and the Antarctic Circumpolar Wave (White and Peterson 1996). Furthermore, it appears that the pupping rate of fur seals at Macquarie Island is related to mean sea surface temperature within the foraging areas of lactating females (Figure 1). However, the influence of oceanographic events on these parameters demands a better understanding of diet, dispersal and reproductive capacity (Testa *et al.* 1991).

#### Irregular or rare ecological catastrophes

There is increasing evidence to suggest that climatological 'anomalies' such as the El Niño-Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO) events are cyclic and may be a long-term and natural feature of the oceans in which marine mammals have evolved (Trillmich 1993). Inhabitants of these regions may therefore have evolved strategies for coping

with most of these events; however, there are instances when events are of such severity that they cause clear impacts at all trophic levels within an ecosystem, including pinnipeds. Most studies of these types of climatological events have described 'catastrophic' effects (negative 'rare ecological events' see Trillmich 1993) rather than 'normal' periodicity.

Catastrophes are defined as either the local extinctions of a meta-population (Ewens *et al.* 1987) or as 'rare, severe environmental events (Hanson and Tuckwell 1987) such as drought, disease or habitat change' (Young 1994). Catastrophic fluctuations in sea temperature, usually associated with events such as ENSO or NAO, can affect many different levels of primary and secondary production. The effects of the NAO occur through trophic levels from primary production to herbivores to predators, influencing growth, life history traits and population dynamics along the way (Ottersen *et al.* 2001). However, the mechanisms thought to underlie the climate-fish recruitment links for NAO remain fairly speculative, making any higher links to fish predators even more tenuous.

One of the best-documented catastrophic environmental events was the severe ENSO event of 1983 that affected much of the eastern coasts of the Americas. The Galapagos fur seal (*A. Galapagoensis*) was impacted heavily by the anomalous environmental conditions during that year (Trillmich and Limberger 1985; Trillmich and Dellinger 1991). There were reductions in pup production, pup weights, and there was complete pup mortality five months after birth. Likewise, mother-dependent yearlings suffered heavy mortality. Female foraging trips were also longer and the number of adults hauled out was lower. There was even a reduction in the mass of the larger males during the subsequent breeding season (Trillmich and Limberger 1985). Loss of whole or high proportions of cohorts through juvenile mortality was also reported in Galapagos sea lions (*Zalophus californianus wolfebaeki*; Trillmich and Dellinger 1991), in South American fur seals and South American sea lions (*Otaria flavescens*; Majluf 1991), California sea lions (*Z. californianus*; Francis and Heath 1991; DeLong *et al.* 1991), northern fur seals (DeLong and Antonelis 1991) and northern elephant seals (*M. angustirostris*; Le Boeuf and Reiter 1991). In Peru, South American fur seals also showed poor pup body condition, and prolonged female foraging trips during the severe ENSO event (Trillmich *et al.* 1986). For a more complete review of the reported effects, see Trillmich and Ono (1991) and Trillmich (1993).

On the other hand, some species of highly mobile, long-lived marine animals may experience less adult mortality during ENSO events than expected from the apparent reductions in localised prey density (Tershy *et al.* 1991). Tershy *et al.* (1991) and Brown and Mate (1983) suggest that marine animals may re-distribute in order to compensate for reduced local productivity, thus giving the impression of a local catastrophe being

responsible for a reduction in abundance (Trillmich 1993; Culik *et al.* 2000). For example, Sydeman and Allen (1999) found that the number of California sea lions ashore peaked during and after major ENSO events.

#### **CURRENT ATTEMPTS TO USE PINNIPEDS AS ECOSYSTEM MONITORS:**

The preceding section has demonstrated that seals can exhibit changes in a number of foraging and reproductive parameters in response to changes in prey distribution and abundance at a range of temporal and spatial scales. The extent and nature of the relationship between any predator and the response of a particular parameter to a change in some aspect of the marine environment is, however, still poorly understood. The use of seals as 'bio-indicators' of anthropogenic environmental change has been limited for two main reasons: 1) the relative unpredictability of a predator's response to environmental change, and 2) the detailed baseline research that is required before these relationships can be understood sufficiently for them to form the basis of a monitoring study. In this section we consider the two types of anthropogenic changes that seals could be used to monitor: 1) large-scale environmental change (mediated by climate change) and 2) smaller-scale changes in ecosystem structure resulting from commercial fishing activities.

Despite the increasing awareness of global climate change, there have been few documented instances of its ecological consequences on pinnipeds. This may be because changes due to increasing temperatures, if any, are still relatively subtle. The measurable changes that have been recorded tend to be in polar regions, and be related to physical changes, such as glacial retreat, or perhaps to lower trophic level organisms such as terrestrial plants or arthropods (Convey 2000). One exception to this is in the Scotia Sea, where changes in krill age structure and reproductive performance have been related to changes in population size, birth mass and reproductive output of Antarctic fur seals (Reid and Croxall 2001). Marine mammals as monitors of large-scale environmental change.

#### **The decline of the Steller sea lion and ecological change in the Northern Pacific Ocean**

The 80% decline in the abundance of a large proportion of the US population of Steller sea lions (*Eumetopias jubata*) since the 1970s stimulated an intensive research program into the potential causes of this decline. The diversity of the research programs aimed at explaining this decline, and their co-ordination across a suite of biological parameters presents an opportunity to examine whether Steller sea lions had the potential to be useful indicators of ecosystem change themselves.

Steller sea lions were abundant throughout their range (California, British Columbia, Gulf of Alaska, Bering Sea including the

Aleutian Island chain) until the 1970s with an estimated population for the western stock in 1956–1960 of 140 000 (Merrick *et al.* 1987). The current estimate for this same stock is now just over 39 000 (Ferrero *et al.* 2000). However, the population decline has not been uniform. Prior to the 1990s, both eastern and western stocks were declining. Currently the Gulf of Alaska (GOA) population is stable, and the Eastern Aleutian Island stock is now actually increasing (York *et al.* 1996). By contrast, the Western Aleutian Island stock was initially declining at 5.9% per year (1975–1985), then the rate of decline peaked between 1985–1990 at 15.6% per year (York *et al.* 1996), and now since 1991 the population is declining at the lower rate of 5% per year (Sease *et al.* 2001).

Steller sea lions are high-level, generalist predators known to consume a wide range of prey species (Merrick *et al.* 1997). The composition of their diet is also known to vary considerably in different areas (Merrick *et al.* 1997). Satellite tracking has demonstrated that there is spatial overlap with specific commercial fisheries (Merrick and Loughlin 1997). We also know from oceanographic and biological data from lower trophic levels that a series of oceanic regime shifts (changes in annual mean sea surface temperature) have occurred in the North Pacific and the Bering Sea over the last century, and that these are concurrent with the changes in Steller sea lion abundance (oceanography: Trenberth 1990; Beamish 1993; Trenberth and Hurrell 1994; Ingraham *et al.* 1998; fish: Anderson and Piatt 1999). We may therefore ask the question, 'Would monitoring aspects of Steller sea lion biology have indicated the occurrence of these oceanic regime shifts?'

The Gulf of Alaska (GOA) and Bering Sea marine ecosystems oscillate between 'warm' climatic regimes and 'cold' climatic regimes (Trenberth 1990; Beamish 1993; Trenberth and Hurrell 1994; Ingraham *et al.* 1998). From 1940–41 through December 1976, the northern Pacific was dominated by an Aleutian Low central pressure anomaly, which intensified from December until May 1977, followed by a shift to a 'warm' regime (Bailey *et al.* 1995). From 1983 to 1989, the Bering Sea and the GOA underwent different temperature changes, with the Bering Sea below normal and the GOA above normal. Another regime shift apparently occurred in 1989.

Annual surveys of Steller sea lion abundance have been done since the late 1970s (Sease *et al.* 2001), and there is a general concordance in rates of change in the different populations with these regime shifts. The most precipitous declines coincide with the 1983–1989 shift, and the area with the greatest rate of decline experiencing a 'cold' regime.

Merrick *et al.* (1997) compared the diversity of Steller sea lion diet in six different regions and found a strong negative correlation between a Diet Diversity Index and the rate of population decline (i.e. the lower the diversity of prey, the higher the rate of

decline). However, the observed differences in diet diversity may simply reflect regional differences in prey availability since little is known about prey selection in this species. Diet studies have been sporadic, and have used different methodologies (Merrick *et al.* 1997). The inherent biases in the different methodologies preclude firm conclusions about diet as an indicator of ecosystem change (Gales and Cheal 1992; Tollit and Thompson 1996; Fea and Harcourt 1997). However, some general changes do appear to be of such magnitude that they have validity. For instance, capelin (*Mallotus villosus*) has reduced in importance compared to a high prevalence in the 1970s, and walleye pollock (*Theragra chalcogramma*) and Atka mackerel (*Pleurogrammus monopterygius*) now dominate the diet in many areas (Merrick *et al.* 1997).

Growth and survival measurements from three separate periods of the decline, 1958, 1975–78 and 1985–86 (Calkins *et al.* 1998), indicate that in 1985 growth was lower and there were increased abortions when the decline was at its worst. York (1994) showed that females were smaller, maturity was delayed, fewer adult females had offspring, and those that did were older in 1985 than those in the mid-1970s. It appears then that body condition indices might be useful monitoring tools. However, recent comparisons by Rea *et al.* (1998) of free-ranging pups in the GOA, AI and southeast Alaska found no indication of poorer body condition in declining populations.

Measurements of at-sea behaviour, including time spent at sea on foraging trips, is limited to studies during the last regime (Merrick *et al.* 1994; Merrick and Loughlin 1997). This element of behaviour has yet to be examined properly with regard to the population decline.

It appears that dramatic changes in Steller sea lion abundance, reproductive output, survival and diet have occurred, with some concordance with known changes in oceanic conditions. Yet despite intense efforts, causal links are still largely at the stage of hypothesis generation. The complexities of the systems combined with logistic difficulties (Steller sea lions are large and dangerous and inhabit inhospitable areas) suggest that Steller sea lions do not offer a straight-forward case for ecosystem monitoring. Further, this highlights that even in intensively studied systems the links between predators and fluctuations in prey availability may not always be clearly identified.

#### **Pinnipeds as monitors of fisheries' effects on target fish species**

There is often assumed to be a close ecological link between some species of seals and commercially exploited fish species. In several large-scale fisheries, such as the Eastern Canadian Atlantic cod fishery, the northern Pacific pollock fishery and the Benguela hake fishery, there is a degree of dietary overlap between the predators and the fishery that could suggest some level of

interaction. Despite the considerable interest, and controversy, associated with these types of interactions (see Chapter 2 and Chapter 4, this volume) there have been almost no attempts to use marine mammals as indicators of fish stock abundance. Most research has rather focussed on whether the seals are having an adverse impact on fishery harvests or fish stock recoveries, or conversely, whether the fishing is having an adverse impact on seal populations. We will examine several of the major studies briefly, even though they may not have been intended specifically to use marine mammals as 'bio-indicators' of fish stocks.

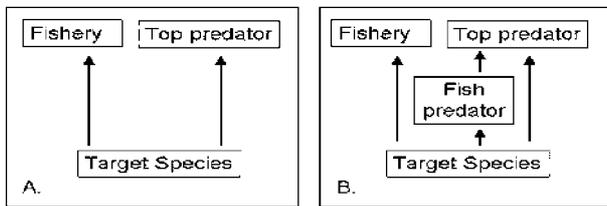
#### **The Atlantic Cod Fishery and interactions with harp and grey seals**

The Atlantic Cod Fishery was once the economic backbone of much of Canada's eastern seaboard (Swain and Sinclair 2000). For much of its several hundred-year history there was vigorous debate on the role of seals (primarily harp seals, *P. groenlandica* and grey seals, *Halichoerus grypus*) in affecting the size of the commercial catch. There was a long-standing view that seals competed directly with the fishery, and that if there were fewer seals, more cod would be available to the fishery. This debate intensified in the 1980s when the annual commercial take of cod declined dramatically, eventually reaching the point that the Canadian government placed a moratorium on all cod fishing until stocks had a chance to recover (Swain and Sinclair 2000). More than a decade later, this moratorium is still in place, and debate has now shifted to the potential for seals to be inhibiting the recovery of the fish stocks (Myers *et al.* 1997; Johnston *et al.* 2000).

The economic significance of the fishery ensured that a considerable body of research was devoted to the problem. The studies were, however, focused on diet and population size, and paid relatively little attention to reproductive parameters such as pup growth and survival.

Nonetheless, there were several key findings that are pertinent to this review. The first was that even though there was some degree of dietary overlap between the seals and the fishery (i. e., the seals did eat the cod species targeted by the fishery) the seals took relatively little cod, with seal predation accounting for only 10–20% of the cod mortality caused by fishing (Mohn and Bowen 1996). Both seals and cod have diverse diets and the ability to modify their diets according to local circumstance.

The other important finding concerned the complexity of the ecological interactions in the marine ecosystem. The simple perception of seals eating cod and therefore reducing the amount of fish available to the fishery assumed that the other multiple links in the trophic pathways were unimportant in determining the outcomes of manipulating the seal component of the model (Yodzis 2000). However, even simple models that incorporated



**Figure 2** (A) The simplistic view of predator and fishery interactions with both taking the target species directly. This view ignores the many other links in the marine ecosystem. (B) The introduction of a single additional fish predator which feeds on the target species, and is also eaten by the top predator. In this case changes in the abundance of the top predator will feedback to the fishery via the fish predator. Increase the number of top predators and the fish predators will decrease, increasing the yield of the target species (adapted from Yodzis 2001).

a single additional cod predator that was also eaten by seals altered the impact of seal predation dramatically (Figure 2). In such a case, reducing seal numbers could actually result in a decline in cod stocks due to increased numbers of the alternate predator (Yodzis 2001).

In conclusion, it is doubtful that seals would have been a useful monitor for the Atlantic cod fishery. This is largely because the seals met few of the criteria needed for a predator species to be a useful monitor (see below). Most notably, the seals seem to have been relatively insensitive to changes in cod stocks, as there were no obvious signs of a demographic response to the dramatic decline in cod numbers despite a relatively high census effort during the years of the decline (Stenson *et al.* 2002). While it is possible that some reproductive parameters that were not monitored may have shown a change (such as pup growth or survival), the pack-ice habitat of the breeding seals would make collection of these data difficult. In any case, the seals are not specialist predators of Atlantic cod, and have a well-developed ability to exploit alternate prey species (Lawson *et al.* 1995; Nilssen *et al.* 1995; Stenson *et al.* 1995).

**Marine mammals as monitors of fisheries' effects on ecosystem structure and function**

**The CCAMLR krill stock management program**

To date, there has only been one attempt to implement a specifically designed and managed program to use the biology of top predators to monitor the abundance of a commercially exploited prey species (see Chapter 3, this volume). The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Ecosystem Monitoring Program (CEMP) was established in 1988, with two specific aims; (i) to detect and record significant changes in critical components of the ecosystem to serve as a basis for the conservation of Antarctic marine living resources and (ii) to distinguish between changes due to harvesting of com-

mercial species and changes due to environmental variability, both physical and biological (CCAMLR 1988).

The program involves monitoring studies on land-based colonies of several species of marine birds and seals located in three Integrated Study Regions; The Antarctic Peninsula, South Georgia, and Prydz Bay, complemented by a number of sites elsewhere in the Antarctic (CCAMLR 1988). The choice of predator species was made following the criteria summarised in Croxall *et al.* (1988). The species selected were: Adelle penguins (*Pygoscelis adeliae*), chinstrap penguins (*P. antarctica*), macaroni penguins (*Eudyptes chrysolophus*), black-browed albatross (*Thalassache melanophrys*), Antarctic petrel (*Thalassoica antarctica*), cape petrel (*Daption capense*), Antarctic fur seal and crabeater seal. Despite the dominance of mammalian predators in terms of numerical abundance and biomass in the Southern Ocean ecosystem, only two of the species being monitored are marine mammals. This is because most mammal species either do not eat commercially exploited prey (such as Weddell seals), or have no terrestrial phase making collection of most performance indices impractical (such as minke (*Balaenoptera bonaerensis*) and other baleen whales). Even basic numerical data on crabeater seals is difficult to collect due to their reliance on pack-ice as year-round habitat.

The CEMP program has produced a large number of studies on various aspects of specific predators' ecological responses to natural environmental fluctuations (e.g. Croxall *et al.* 1999; Reid *et al.* 1999; Reid and Croxall 2001). There have also been a number of models devised to help with management (Croll and Tershy 1998; Thompson *et al.* 2000), but there has yet to be a critical assessment of whether the principal aims of the program are being met. Particularly important are studies that attempt to measure the functional response of predators to fluctuations in krill stocks. This has only been done in a few studies and locations, and in almost all case the temporal series is short. To date, Guinet *et al.* (2001) and Harcourt *et al.* (2001) are the only studies relating mammalian predator performance to concurrent and dedicated prey surveys. Seabird studies at South Georgia have demonstrated poor performance in terms of several monitoring parameters in a year of low krill abundance in the area (Croxall *et al.* 1999), but only two years of krill survey data are available.

There have also been relatively few studies that have examined the relationship between fisheries and top predators explicitly. A key step is to establish the extent of the spatial and temporal overlap of fisheries and predators. Despite the large number of predators in the Southern Ocean ecosystem, only a few have compared the spatial use of a predator with a fishery (e.g., van den Hoff *et al.* 2002). Ichii and Kato (1991) concluded that there was little overlap between the South Shetland Island krill fishery and the resident penguin population because there was little spatial overlap; the penguins were feeding at different

depths to those used by the trawlers, and the penguins and the fishery were catching different sized kill. Croll and Tershy (1998) regarded this as overly simplistic and pointed out that the dynamic nature of krill swarms mean that even fishing in an area adjacent to predator foraging grounds can reduce prey availability due to reduced advection of prey into the birds' foraging areas. However, it is important to recognise that these studies investigated the relationships at markedly different spatial scales.

A major challenge for CEMP is detecting current anthropogenically induced changes from the confounding effects of past ecosystem perturbations. Perhaps the most important is the largely unknown response of Antarctic krill predators to the large-scale declines in whale numbers in the twentieth century (Chapter 3, this volume). Laws (1977) estimated that the harvest of Antarctic baleen whales released up to 80 million tonnes of krill annually. There is some evidence that other krill predators have reacted to this major ecosystem perturbation through increased abundance and increased fecundity (penguins, fur seals, crabeater seals and minke whales). However, the true nature and full extent of the predator response is difficult to determine due to the lack of baseline data for most species, the difficulty in obtaining abundance or reproductive data for many of these species, and the concurrent and confounding effect of local climate change. Any measurable change in predator population in the future must take into account that the Antarctic ecosystem, even in the absence of a krill fishery, may already have been experiencing important fundamental adjustments in community structure.

#### Recent declines in southern elephant seal populations

Southern elephant seals represent an example of a marine mammal demonstrating a clear change in a key performance indicator (population size), but one that has yet to be attributable to any specific causal factor. Southern elephant seals have been exhibiting long-term population declines in two of their four major breeding areas since the 1950s, with rates of decline ranging between 2–8% annually (Laws 1994). A number of causal agents have been investigated, and several, such as human disturbance at colonies (Engelhard *et al.* 2001, 2002), paucity of males and fishing activity have been dismissed (Hindell *et al.* 1991). Some studies have identified differences in age-specific mortality as a likely proximate cause (Hindell 1991; McMahon *et al.* 1999, 2000); however, the underlying factors driving these changes are still not understood despite several decades of research.

The elephant seal situation makes an important and salutary point when considering the role of marine mammals as monitors of ecological change. It is not sufficient to demonstrate that a species, or population, is capable of responding to changes in environmental circumstances in a measurable way. It is also vital

that the ecological links between the measured parameters of the predator and the associated environmental parameters are understood sufficiently to enable correct interpretation of the observed responses. For the southern elephant seal, this is clearly not the case. These animals are sending some kind of signal about the ecosystem that they inhabit, but we have not yet been able to decipher the message.

#### WHAT SPECIES AND PARAMETERS ARE THE MOST USEFUL TO MONITOR?

Croxall *et al.* (1988) outlined a useful set of criteria to identify parameters to measure when designing monitoring studies, but there has been little refinement of their conclusions in the intervening years. The following section re-iterates many of the conclusions drawn by Croxall *et al.* (1988), but with an emphasis on an application to more general studies. Croxall *et al.* (1988) focussed on a specific, krill-based ecosystem; we have broadened the scope of their recommendations.

We have demonstrated that different species of pinniped, and elements of their physiology, behaviour and ecology, respond to environmental variation in differing ways. However, this alone is insufficient to make a particular species useful as a meaningful indicator, and two questions still need to be addressed: (i) what species are most likely to demonstrate some kind of measurable change in response to altered environmental conditions and (ii) what parameters could be expected to respond to environmental variation so that they are both detectable and of biological significance to the species or community under investigation?

#### Choice of species

Equally important are the accessibility of the species and ease and accuracy of data collection (Croxall *et al.* 1988). This usually requires large samples and parameters sensitive to changes in food availability (Croxall *et al.* 1988). Minke whales and crabeater seals are both krill specialists, but neither has a terrestrial phase, making collection of information on reproductive performance difficult. However, as technology improves, satellite linked data loggers may be used to provide data on important aspects of foraging behaviour (e.g. Bradshaw *et al.* 2002). The most useful monitoring species are those with specialised diets as this reduces the probability of compensatory behaviour masking temporal or spatial trends. For example, krill-specialist predators have an advantage for CCAMLR monitoring studies (e.g. Antarctic fur seals at South Georgia, crabeater seals, minke whales (Croxall *et al.* 1988)) since their responses to environmental variation are more easily interpretable. At the other extreme, Harcourt *et al.* (2001) and Harcourt *et al.* (2002) concluded that the at-sea behaviour of generalist predators capable of opportunistic feeding (e.g. New Zealand fur seals) makes these species inappropriate as a tool for monitoring temporal variation.

### Choice of parameters

Possible candidates include parameters that measure:

- 1 Individual performance attributes such as survival, body condition, disease status, reproductive output
- 2 Individual behavioural attributes such as dive effort, movement patterns and rates, diet
- 3 Demographic attributes such as population trends, abundance, distribution, emigration/immigration

### Individual performance parameters

Reproductive success, as measured by offspring condition or survival, may be a useful index of local environmental influences (Doidge *et al.* 1984). Elevated rates of neonatal or immediately post-natal mortality may be important responses, since most normal mortality occur in the first year of life (Croxall *et al.* 1988). However, in as much as survival and fecundity rates are of importance for the demography of populations, apart from neonatal mortality, they tend to be of low suitability for monitoring programmes because of the long lag times (5–15 years) and the large samples required to detect significant changes (Croxall *et al.* 1988).

Weaning mass may be a useful index of maternal foraging success. Food supply for phocids before lactation, or during lactation for otariids, or for the weaned pup at independence, could have direct consequences for survival and reproductive success (Boyd 1991). Weaning mass of male northern fur seals, a function of maternal foraging success prior to weaning, is related to post-weaning survival to four years of age (Baker and Fowler 1992). Both Hall *et al.* (2001) for grey seals, and McMahon *et al.* (2000) for southern elephant seals, found that weaning mass influenced the probability of first-year survival. For these phocids, this relationship suggests that resource accumulation by mothers prior to lactation is related to their future reproductive success. Thus, Hall *et al.* (2001) suggested that average survival of grey seal pups will vary from year to year depending on the average condition of breeding females.

Trites and Bigg (1996) warned that the strong seasonal and regional components of growth should be taken into account when assessing the role of pinnipeds as energy consumers in the ecosystem. Croxall *et al.* (1988) also warned that there is usually substantial individual variation in growth rates, so that once again, large samples are needed. Here, annual synchrony in pupping dates is important to reduce extra variation due to weighing large samples of pups at intervals (Croxall *et al.* 1988). Boyd *et al.* (1997) suggested that due to compensatory effects of foraging behaviour, the measurement of growth rates is likely to be relatively insensitive to variation in the foraging conditions of mothers compared with behavioural parameters such as foraging trip duration. Serial measurements of known-age individuals over-

come biases resulting from cross-sectional measurements (Croxall *et al.* 1988; Lunn and Boyd 1993; Trites 1993).

Measuring adult mass directly is also possible, but there is usually substantial variation in adult mass, so again large samples are required (Croxall *et al.* 1988). For most seals, these data are more difficult to obtain due to the difficulty of capturing and manipulating large adults. Where adults can be captured, assessing relative body condition may be more important than measuring mass (Gales and Burton 1987; Croxall *et al.* 1988; Tierney *et al.* 2001).

### Behavioural parameters

The monitoring of behavioural changes such as foraging trip duration or the number of foraging trips, may be useful for species that need to return regularly to land to suckle their pups, so long as trip durations do not exhibit markedly discontinuous distributions (Croxall *et al.* 1988; Goldsworthy 1999). However, large sample sizes are usually required to achieve statistical validity (Croxall *et al.* 1988; Harcourt *et al.* 2001). Data on foraging trips are generally less useful for phocids, many species of which stay ashore with their pups during their brief lactation. Outside the breeding season, phocid seals are not constrained to return to land and so the inherent flexibility in this behaviour would make it difficult to detect extrinsically induced changes.

Activity budgets at sea may, however, be good estimates of local environmental variation, provided the instruments used to collect data at sea do not modify predator behaviour and many individuals can be instrumented within one season (Croxall *et al.* 1988). Quantifying diving behaviour variables such as the proportion of time spent diving, the relative dive effort, or time spent at depth may also provide insights into compensatory behaviour used by predators that may mask changes in other parameters. For certain species, the appropriate choice of age class can improve the ability to detect change. For example, the diving limitation of naïve elephant seals during their first foraging trip (i.e. restricted to shallower depths) may make this age class more susceptible to large-scale oceanographic variations that render prey more difficult to acquire in some years (Hindell *et al.* 1999).

### Demographic parameters

Changes in the number of animals in a population or in the survival of individuals in that population are arguably the least ambiguous of all the parameters. From a monitoring perspective, population size is often the simplest to estimate, as it simply requires a census of pups born at a key time in the year. This is an ideal parameter for terrestrial, colonial breeding species, such as the otariids and monacine seals. However, as the southern elephant seal and the Steller sea lion examples indicated, establishing a causal link between population changes and a specific environmental change can be difficult.

Information on demographic performance (individual survival and recruitment into the breeding population), may be the best ultimate indicator of a response to environmental change. Such data are notoriously difficult to collect for long-lived species such as pinnipeds, as they require long-term studies following the individual histories of a large number of marked individuals in the population. The long-term nature of these studies precludes these parameters as useful indicators, except in specific circumstances. For example, the studies may already be established and on-going, in which case demographic studies will be powerful tools. Alternatively, some cross-sectional demographic studies may also provide helpful insights, such as aging studies that may indicate shifts in age structure. If teeth are used to age individuals, relative changes in the number and thickness of growth layers can also provide useful information on historical changes in some aspects of the seal's biology.

## CONCLUSIONS

Although the notion of using top predators to monitor changes occurring at lower trophic levels has often been postulated as a cost-effective and practical method for monitoring human-induced ecosystem changes, there are few examples of this being applied successfully to pinnipeds. That several, easily measurable parameters do vary in response to natural variation in food supply has been demonstrated at several spatial and temporal scales. However, these studies also indicate the complexities involved in attempting to make simple associations between a measurable response of a predator and specific elements of the environment.

Many seal species are integral parts of complex marine ecosystems, and as such it needs to be recognised that many factors will be interacting to produce any response variable chosen to measure performance. The intricacies of these interactions are well illustrated by the difficulties in predicting changing trophic links with changes in prey abundance, exemplified in several large-scale fisheries. Recent analyses of long-term data collected as part of the CCAMLR ecosystem monitoring program have suggested that integrating information from a number of species and a range of variables simultaneously may better than single species approach (De la Mare and Constable 2000; Boyd and Murray 2001).

Nonetheless, under circumstances where long-term, multi-species data sets are unavailable, some pinnipeds can be used to measure anthropogenic change. It is the degree to which they can be useful which depends on a number of factors. These include, but are not restricted to, the temporal and spatial scales of the effect to be monitored, the ecological characteristics of the seal species, and the nature of the anthropogenic agent. Regardless of the choice of best behavioural or demographic parameters required to measure environmental variation, extensive moni-

toring programmes should not be started unless there are ongoing complementary, long-term studies of the fundamental demographic processes, because knowledge of these will be essential to the interpretation of monitoring results (Croxall *et al.* 1988).

One of the reasons that marine ecologists appear not to have made much progress with regard to the issues discussed in this chapter is that many studies have failed to make the distinction between species-specific (i.e. conservation-based) aims and those directed towards understanding ecosystem processes. Much of our research is designed to focus on more immediate conservation outcomes associated with preserving species. However, long-lived marine vertebrate populations are likely to respond to longer-term environmental processes that can only be assessed and monitored with a set of explicit hypotheses to test the effects of environmental variability on predator performance. There is still an over-riding need to identify the *mechanisms* underlying hypothesised relationships. We therefore recommend that researchers, management authorities and funding agencies focus less on species-specific issues and invest in well-planned, broad-scale ecosystem research to address these issues simultaneously.

Our conclusions have identified important research aims, and it is clear that these aims must still embrace the fundamental concept that in order to determine the underlying processes which dictate predator performance, long-term monitoring studies are essential to provide a greater understanding of ecological mechanism. This remains the highest priority in marine ecosystem research. Further, the nature of environmental variability is complex, with spatial and temporal effects often intertwined. It is important therefore in the design of marine ecology studies that there be adequate spatial and temporal replication to tease apart these confounding effects.

Finally, we recommend that when implementing studies with these aims, researchers must address the uncertainties associated with statistical power. That is, it is important to identify the magnitude of environmental change (whether it is natural, human-induced or both) required to *detect* a measurable change in predator performance. We also stress that temporal, spatial and sample replication are paramount to achieve the aims of broad-scale studies investigating the effects of environmental variation on marine predators.

## REFERENCES

- Abbott, M., and B. Barksdale. (1995). Variability in upwelling systems as observed by satellite remote sensing. In *Upwelling in the ocean: modern processes and ancient records*. (Eds C. Summerhayes, K. -C. Emeis, M. V. Angel, R. L. Smith and B. Zeitzschel.) pp. 221–238. John Wiley and Sons, Berlin.

- Anderson, P. J., and Piatt, J. F. (1999). Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series* **189**, 117–123.
- Bailey, K. M., Macklin, S. A., Reed, R. K., Brodeur, R. D., Ingraham, W. J., Piatt, J. F., Shima, M., Francis, R. C., Anderson, P. J., Royer, T. C., Hollowed, A. B., Somerton, D. A., and Wooster, W. S. (1995). ENSO events in the northern Gulf of Alaska, and effects on selected marine fisheries. *California Cooperative Oceanic Fisheries Investigations Reports* **36**, 78–96.
- Baker, J. D., and Fowler, C. W. (1992). Pup weight and survival of northern fur seals *Callorhinus ursinus*. *Journal of Zoology, London* **227**, 231–238.
- Banks, H. T., Wood, R. A., Gregory, J. M., Johns, T. C., and Jones, G. S. (2000). Are observed decadal changes in intermediate water masses a signature of anthropogenic climate change? *Geophysical Research Letters* **27**, 2961–2964.
- Beamish, R. J. (1993). Climate and exceptional fish production off the west coast of North America. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 2270–2291.
- Bengtson, J. L. (1988). Long-term trends in the foraging patterns of female Antarctic fur seals at South Georgia. In *Antarctic Ocean and resources variability*. (Ed. D. Sahrhage.) pp. 286–291. Springer-Verlag: Berlin.
- Bonner, W. N. (1968). The fur seal of South Georgia, Rep. No. 56. British Antarctic Survey, London.
- Boyd, I. L. (1991). Environmental and physiological factors controlling the reproductive cycles of pinnipeds. *Canadian Journal of Zoology* **69**, 1135–1148.
- Boyd, I. L., and Ambom, T. (1991). Diving behaviour in relation to water temperature in the southern elephant seal: foraging implications. *Polar Biology* **11**, 259–266.
- Boyd, I. L., Amould, J. P. Y., Barton, T., and Croxall, J. P. (1994). Foraging behaviour of Antarctic fur seals during periods of contrasting prey abundance. *Journal of Animal Ecology* **63**, 703–713.
- Boyd, I. L., McCafferty, D. J., and Walker, T. R. (1997). Variation in foraging effort by lactating Antarctic fur seals: response to simulated increased foraging costs. *Behavioral Ecology and Sociobiology* **40**, 135–144.
- Boyd, I. L., and Murray, A. W. A. (2001). Monitoring a marine ecosystem using responses of upper trophic level predators. *Journal of Animal Ecology* **70**, 747–760.
- Boyd, I. L., Hawker, E. J., Brandon, M. A., and Staniland, I. J. (2001). Measurement of ocean temperatures using instruments carried by Antarctic fur seals. *Journal of Marine Systems* **27**, 277–288.
- Bradshaw, C. J. A., Davis, L. S., Lallas, C., and Harcourt, R. G. (2000). Geographic and temporal variation in the condition of pups of the New Zealand fur seal (*Arctocephalus forsteri*): evidence for density dependence and differences in the marine environment. *Journal of Zoology, London* **252**, 41–51.
- Bradshaw, C. J. A., Hindell, M. A., Littnan, C., and Harcourt, R. G. (2002). (In press). Determining marine movements of Australasian pinnipeds. In *Evolution and Biogeography of Australasian Vertebrates*. (Eds R. Merriam, M. Archer, G. Hickey, and M. Lee.) Australian Scientific Publishers: Sydney.
- Brown, R. F., and Mate, B. R. (1983). Abundance, movements, and feeding habits of harbor seals, *Phoca vitulina*, at Netarts and Tillamook Bays, Oregon. *Fishery Bulletin* **81**, 291–301.
- Burton, H. R. (1998). Long-term changes in first-year mortality of two seal species: southern elephant seals from Macquarie Island and Weddell seals from the Vestfold Hills. *New Zealand Natural Sciences* **23** (Supplement), 25.
- Calkins, D. G., Becker, E. F., and Pitcher, K. W. (1998). Reduced body size of female steller sea lions from a declining population in the Gulf of Alaska. *Marine Mammal Science* **14**, 232–244.
- Campagna, C., Rivas, A. L., and Rosa Marin, M. (2000). Temperature and depth profiles recorded during dives of elephant seals reflect distinct ocean environments. *Journal of Marine Systems* **24**, 299–312.
- CCAMLR. (1988). CCAMLR Ecosystem Monitoring Program: Standard Methods for Monitoring Parameters of Predatory Species CCAMLR.
- Convey, P. (2000). Environmental change and Antarctic terrestrial life histories: fact and prediction. In *Antarctic Ecosystems: Models for a wider Ecological Understanding*. (Eds W. Davison, C. Howard-Williams and P. Broady.) pp. 243–251. Caxton Press, Christchurch.
- Costa, D. P., and Gentry, R. L. (1986). Free-ranging energetics of northern fur seals. In *Fur seals: maternal strategies on land and at sea*. (Eds R. L. Gentry and G. L. Kooyman.) pp. 79–101. Princeton University Press: Princeton.
- Costa, D. P. (1993). The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia. *Symposium Zoological Society of London* **66**, 293–314.
- Costa, D. P., Croxall, J. P., and Duck, C. D. (1989). Foraging energetics of Antarctic fur seals in relation to changes in prey availability. *Ecology* **70**, 596–606.
- Croll, D. A., and Tershy, B. R. (1998). Penguins, fur seals, and fishing: prey requirements and potential competition in the South Shetland Islands, Antarctica. *Polar Biology* **19**, 365–374.
- Croxall, J. P., McCann, T. S., Prince, P. A., and Rothery, P. (1988). Reproductive performance of seabirds and seals at South Georgia and Signy Islands, 1976–1987: implications for southern ocean monitoring studies. In *Antarctic Ocean and Resource Variability*. (Ed. D. Sahrhage.) pp. 261–285. Springer-Verlag, Berlin.
- Croxall, J. P., Reid, K., and Prince, P. A. (1999). Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. *Marine Ecology-Progress Series* **177**, 115–131.
- Culik, B., Hennicke, J., and Martin, T. (2000). Humboldt penguins out manoeuvring El Niño. *Journal of Experimental Biology* **203**, 2311–2322.
- De la Mare, W. K., and Constable, A. J. (2000). Utilising data from ecosystem monitoring for monitoring fisheries: Development of statistical summaries of indices arising from the CCAMLR Ecosystem Monitoring Program. *CCAMLR Science* **7**, 101–118.
- DeLong, R. L., and Antonelis, G. A. (1991). Impact of the 1982–1983 El Niño on the northern fur seal population at San Miguel Island, California. In *Pinnipeds and El Niño: Responses to environmental stress*. (Eds F. Trillmich and K. A. Ono). Vol. 88, pp. 75–83. Springer-Verlag, Berlin.
- DeLong, R. L., Antonelis, G. A., Oliver, G. W., Stewart, B. S., Lowry, M. S., and Yochem, P. K. (1991). Effects of the 1982–1983 El Niño on several population parameters and diet of California sea lions on the California Channel Islands. In *Pinnipeds and El Niño: Responses*

- to environmental stress. (Eds F. Trillmich and K. A. Ono). Vol. 88, pp. 166–172. Springer-Verlag, Berlin.
- Doidge, D. W., Croxall J. P., and Baker J. R. (1984). Density-dependent pup mortality in the Antarctic fur seal *Arctocephalus gazella* at South Georgia. *Journal of Zoology (London)* **202**, 449–460.
- Doidge, D. W., and Croxall J. P. (1985). Diet and energy budget of the Antarctic fur seal *Arctocephalus gazella* at South Georgia. In *Antarctic nutrient cycles and food webs*. (Eds W. R. Siegfried, P. R. Condy, and R. Laws.) pp. 543–550. Springer-Verlag: Berlin.
- Doidge, D. W., McCann T. S., and Croxall J. P. (1986). Attendance behavior of Antarctic fur seals. In *Fur seals Maternal strategies on land and at sea*. (Eds R. L. Gentry and G. L. Kooyman.) pp. 102–114. Princeton University Press: Princeton.
- Duck, C. D. (1990). Annual variation in the timing of reproduction in Antarctic fur seals, *Arctocephalus gazella*, at Bird Island, South Georgia. *Journal of Zoology (London)* **222**, 103–116.
- El-Sayed, S. Z. (1988). Productivity of the Southern Ocean: a closer look. *Comparative Biochemical Physiology* **90B**, 489–498.
- Engelhard, G. H., van den Hoff, J., Broekman, M., Baarspul, A. N. J., Field, I., Burton, H. R., and Reijnders, P. J. H. (2001). Mass of weaned elephant seal pups in areas of low and high human presence. *Polar Biology* **24**, 244–251.
- Ewens, W. J., Brockwell, P. J., Gan, J. M., Resnick, S. I., and Resnick, D. (1987). Minimum viable population size in the presence of catastrophes. In *Viable populations for conservation*. (Ed. M. E. Soulé.) pp. XXX–XXX. Cambridge University Press: Cambridge.
- Engelhard, G. H., Brasseur, S. M. J. M., Hall, A. J., Burton, H. R., and Reijnders, P. J. H. (2002). Adrenocortical responsiveness in southern elephant seal mothers and pups during lactation and the effect of scientific handling. *Journal of Comparative Physiology – B, Biochemical, Systemic, and Environmental Physiology* **172**, 315–328.
- Fea, N., and Harcourt, R. (1997). Assessing the use of faecal and regurgitate analysis as a means of determining the diet of New Zealand fur seals. In *Marine mammal research in the southern hemisphere*. (Eds M. Hindell and C. Kemper.) pp. 143–150. Surrey Beatty and Sons, Chipping Norton.
- Ferrero, R. C., DeMaster, D. P., Hill, P. S., Muto, M. M., and Lopez, A. L. (2000). Alaska marine mammal stock assessments, 2000, NOAA Technical Memorandum NMFS-AFSC-119. Pages 191–243. U. S. Department of Commerce, NOAA.
- Field, I., Hindell, M. A., Slip, D. J., and Michael, K. J. (2001). Foraging strategies of southern elephant seals (*Mirounga leonina*) in relation to frontal zones and water masses. *Antarctic Science* **13**, 371–379.
- Francis, J. M., and Heath, C. B. (1991). The effects of El Niño on the frequency and sex ratio of suckling yearlings in the California sea lion. In *Pinnipeds and El Niño: Responses to environmental stress*. (Eds F. Trillmich and K. A. Ono). Vol. 88, pp. 193–201. Springer-Verlag, Berlin.
- Furness, R. W., and Tasker M. L. (2000). Sea-bird fishery interactions: quantifying the sensitivity of seabirds to reductions in sand eel abundance and identification of key areas for sensitive seabirds in the North Sea. *Marine Ecology Progress Series* **202**, 253–264.
- Gales, N. J., and Burton H. R. (1987). Ultrasonic measurement of blubber thickness of the southern elephant seal *Mirounga leonina* (Linn.). *Australian Journal of Zoology* **35**, 207–217.
- Gales, N. J., and Cheal, A. J. (1992). Estimating diet composition of the Australian Sea-lion (*Neophoca cinereus*) from scat analysis: an unreliable technique. *Wildlife Research* **19**, 447–456.
- Gales, R., Pemberton, D., Lu, C. C., and Clarke, M. R. (1993). Cephalopod diet of the Australian fur seal – variation due to location, season, and sample type. *Australian Journal of Marine and Freshwater Research* **44**, 657–671.
- Gentry, R. L., and Kooyman, G. L. (Eds) (1986). *Fur seals: maternal strategies on land and at sea*. Princeton University Press, Princeton.
- Georges, J. -Y., Bonadonna, F., and Guinet C. (2000). Foraging habitat and diving activity of lactating subantarctic fur seals in relation to sea-surface temperatures at Amsterdam Island. *Marine Ecology Progress Series* **196**, 291–304.
- Georges, J. -Y., and Guinet C. (2000). Early mortality and peri-natal growth in the subantarctic fur seal (*Arctocephalus tropicalis*) on Amsterdam Island. *Journal of Zoology, London* **251**, 277–287.
- Goldsworthy, S. D. (1999). Maternal attendance behaviour of sympatrically breeding Antarctic and subantarctic fur seals, *Arctocephalus* spp., at Macquarie Island. *Polar Biology* **21**, 316–325.
- Green, K., and Burton, H. R. (1987). Seasonal and geographical variation in the food of Weddell seals, *Leptonychotes weddelli*, in Antarctica. *Australian Wildlife Research* **14**, 475–489.
- Green, K., Williams R., and Burton, H. R. (1997). Foraging ecology of Antarctic fur seals *Arctocephalus gazella* around Heard Island. In *Marine mammal research in the Southern Hemisphere*. (Eds M. Hindell and C. Kemper.) pp. 105–113 Surrey Beatty and Sons, Chipping Norton.
- Guinet, C., Dubroca, L. Lea, M. A., Goldsworthy, S., Chereil, Y., Duhamel, G. Bonadonna, F., and Donnay, J. -P. (2001). Spatial distribution of the foraging activity of Antarctic Fur seal *Arctocephalus gazella* females in relation to oceanographic factors: a scale dependant approach using geographic information systems. *Marine Ecology Progress Series* **219**, 251–264.
- Hall, A. J., Watkins, J., and Hammond P. S. (1998). Seasonal variation in the diet of harbour seals in the south-western North Sea. *Marine Ecology Progress Series* **170**, 269–281.
- Hall, A. J., McConnell, B. J., and Barker R. J. (2001). Factors affecting first-year survival in grey seals and their implications for life history strategy. *Journal of Animal Ecology* **70**, 138–149.
- Hanson, F. B., and Tuckwell, H. C. (1987). Persistence times of populations with large random fluctuations. *Theoretical Population Biology* **14**, 46–61.
- Harcourt, R. G., Bradshaw, C. J. A., and Davis L. S. (2001). Summer foraging behaviour of a generalist predator, the New Zealand fur seal (*Arctocephalus forsteri*). *Wildlife Research* **28**, 599–606.
- Harcourt, R. G., Bradshaw, C. J. A., Dickson, K., and Davis, L. S. (2002). Foraging ecology of a generalist predator, the female New Zealand fur seal. *Marine Ecology Progress Series* **227**, 11–24.
- Härkönen, T. (1987). Seasonal and regional variations in the feeding habits of the harbour seal, *Phoca vitulina*, in the Skagerrak and the Kattegat. *Journal of Zoology, London* **213**, 535–543.
- Hindell, M. A. (1991). Some life history parameters of a declining population of southern elephant seals, *Mirounga leonina*. *Journal of Animal Ecology* **60**, 119–134.
- Hindell, M. A., Burton, H. R., and Slip, D. J. (1991). Foraging grounds of southern elephant seals, *Mirounga leonina*, as inferred from water

- temperature data. *Australian Journal of Marine and Freshwater Research* **42**, 115–128.
- Hindell, M. A., McConnell, B. J., Fedak, M. A., Slip D. J., Burton H. R., Reijnders P. J. H., and McMahon C. R. (1999). Environmental and physiological determinants of successful foraging by naive southern elephant seal pups during their first trip to sea. *Canadian Journal of Zoology* **77**, 1807–1821.
- Hunt, G. L., Heinemann D., and Everson I. (1992). Distribution and predator-prey interactions of macaroni penguins, Antarctic fur seals, and Antarctic krill near Bird Island, South Georgia. *Marine Ecology Progress Series* **86**, 15–30.
- Ichii, T., and Kato, H. (1991). Food and daily food consumption of southern minke whales in the Antarctic. *Polar Biology* **11**, 479–487.
- Ingraham, W. J., Ebesmeyer, C. C., and Hinrichsen, R. A. (1998). Imminent climate and circulation shift in northeast Pacific ocean could have major impact on marine resources. *EOS, Transactions, American Geophysical Union* **79**, 197.
- Jaksic, F. M. (1998). The multiple facets of El Niño/Southern Oscillation in Chile. *Revista Chilena de Historia Natural* **71**, 121–131.
- Jaquet, N., Whitehead H., and Lewis M. (1996). Coherence between 19th century sperm whale distributions and satellite derived pigments in the tropical Pacific. *Marine Ecology-Progress Series* **145**, 1–10.
- Johnston, D. W., Meisenheimer, P., and Lavigne D. M. (2000). An evaluation of management objectives for Canada's commercial harp seal hunt, 1996–1998. *Conservation Biology* **14**, 729–737.
- Klages, N. T. W., and Bester, M. N. (1998). Fish prey of fur seals *Arctocephalus* spp. at subantarctic Marion Island. *Marine Biology* **131**, 559–566.
- Laws, R. M. (1984). Seals. In *Antarctic Ecology*. (Ed. R. M. Laws.) pp. 621–716. Academic Press: London.
- Laws, R. M. (1977). Seals and whales of the Southern Ocean. *Philosophical transcripts of the Royal Society of London B* **279**, 81–96.
- Laws, R. M. (1994). History and present status of southern elephant seal populations. In *Elephant seals: population ecology, behavior and physiology*. Eds B. J. Le Boeuf and R. M. Laws. pp. 49–65. University of California Press, Berkeley.
- Lawson, J. W., Stenson, G. B., and McKinnon, D. G. (1995). Diet of harp seals (*Phoca groenlandica*) in nearshore waters of the northwest Atlantic during 1990–1993. *Canadian Journal of Zoology* **73**, 1805–1818.
- Lea, M. A., Hindell, M. A. Guinet, C., and Goldsworthy, S. D. (2002). Variability in the diving activity of Antarctic fur seals, *Arctocephalus gazella*, at Iles Kerguelen. *Polar Biology* **25**, 269–279.
- Le Boeuf, B. J., and Reiter, J. (1991). Biological effects associated with El Niño, Southern Oscillation 1982–1983, on northern elephant seals breeding at Año Nuevo, California. In *Pinnipeds and El Niño: Responses to environmental stress*. (Eds F. Trillmich and K. A. Ono). Vol. 88, pp. 206–218. Springer-Verlag, Berlin.
- Lima, M., and Páez, E. (1995). Growth and reproductive patterns in the South American fur seal. *Journal of Mammalogy* **76**, 1249–1255.
- Lunn, N. J., and Boyd, I. L. (1993). Effects of maternal age and condition on parturition and the perinatal period of Antarctic fur seals. *Journal of Zoology (London)* **229**, 55–67.
- Majluf, P. (1991). El Niño effects on pinnipeds in Peru. In *Pinnipeds and El Niño: Responses to environmental stress*. (Eds F. Trillmich and K. A. Ono). Vol. 88, pp. 55–65. Springer-Verlag, Berlin.
- McMahon, C. R., Burton, H. R., and Bester, M. N. (1999). First year survival of southern elephant seals, *Mirounga leonina* at Macquarie Island. *Polar Biology* **21**, 279–284.
- McMahon, C. R., Burton H. R., and Bester, M. N. (2000). Weaning mass and the future survival of juvenile southern elephant seals, *Mirounga leonina*, at Macquarie Island. *Antarctic Science* **12**, 149–153.
- Merrick, R. L., Chumbley, M. K., and Byrd, G. V. (1997). Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: A potential relationship. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 1342–1348.
- Merrick, R. L., and Loughlin, T. R. (1997). Foraging behavior of adult female and young-of-the-year Steller sea lions in Alaskan waters. *Canadian Journal of Zoology* **75**, 776–786.
- Merrick, R. L., Loughlin, T. R., Antonelis, G. A., and Hill, R. (1994). Use of satellite-linked telemetry to study steller sea lion and northern fur seal foraging. *Polar Research* **13**, 105–114.
- Merrick, R. L., Loughlin, T. R., and Calkins, D. G. (1987). Decline in Abundance of the Northern Sea Lion *Eumetopia jubatus* in Alaska USA 1956–86. *U S National Marine Fisheries Service Fishery Bulletin* **85**, 351–366.
- Mohn, R., and Bowen, W. D. (1996). Grey seal predation on the eastern Scotia Shelf: modelling the impact on Atlantic cod. *Canadian journal of Fisheries and Aquatic Science* **53**, 2722–2738.
- Myers, R. A., Hutchings, J. A., and Barrowman, N. J. (1997). Why do fish stocks collapse – the example of cod in Atlantic Canada. *Ecological Applications* **7**, 91–106.
- Nicol, S., Pauly, T., Bindoff, N. L., Wright, S., Thiele, D., Hosie, G. W., Strutton, P. G. P. G., and Woehler, E. (2000). Ocean circulation off East Antarctica affects ecosystem structure and sea-ice extent. *Nature* **406**, 504–507.
- Nilssen, K. T., Haug, T., Potelov, V., and Timoshenko Y. K. (1995). Feeding habits of harp seals (*Phoca groenlandica*) during early summer and autumn in the northern Barents sea. *Polar Biology* **15**, 485–493.
- Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P. C., and Stenseth, N. C. (2001). Ecological effects of the North Atlantic Oscillation. *Oecologia* **128**, 1–14.
- Priddle, J., Boyd, I. L., Whitehouse, M. J., Murphy, E. J., and Croxall, J. P. (1998). Estimates of Southern Ocean primary production – constraints from predator carbon demand and nutrient drawdown. *Journal of Marine Systems* **17**, 275–288.
- Rea, L. D., Castellini, M. A., Fadely, B. S., and Loughlin, T. R. (1998). Health status of young Alaska steller sea lion pups (*Eumetopias jubatus*) as indicated by blood chemistry and hematology. *Comparative Biochemistry and Physiology Part A*, 617–623.
- Read, A. J. (1990). Estimation of body condition in harbour porpoises. *Canadian Journal of Zoology* **68**, 1962–1966.
- Reid, K. (1995). The diet of Antarctic fur seals (*Arctocephalus gazella* Peters 1875) during winter at South Georgia. *Antarctic Science* **7**, 241–249.
- Reid, K., and Amould, J. P. Y. (1996). The diet of Antarctic fur seals *Arctocephalus gazella* during the breeding season at South Georgia. *Polar Biology* **16**, 105–114.
- Reid, K., and Croxall, J. P. (2001). Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem. *Proceedings of the Royal Society of London – Series B: Biological Sciences* **268**, 377–384.

- Reid, K., Watkins, J. L., Croxall, J. P., and Murphy, E. J. (1999). Krill population dynamics at South Georgia 1991–1997, based on data from predators and nets. *Marine Ecology-Progress Series* **177**, 103–114.
- Rindorf, A., Wanless, I. S., and Harris M. P. (2000). Effects of changes in sandeel availability on the reproductive output of seabirds. *Marine Ecology Progress Series* **202**, 241–252.
- Rounsevell, D., and Eberhard I. (1980). Leopard seals, *Hydrurga leptonyx* (Pinnipedia), at Macquarie Island from 1949 to 1979. *Australian Wildlife Research* **7**, 403–415.
- Sease, J. L., Taylor, W. P., Loughlin, T. R., and Pitcher, K. W. (2001). Aerial and land-based surveys of Steller sea lions (*Eumetopias jubata*) in Alaska, June and July 1999 and 2000. NOAA Technical Memorandum NMFS-AFSC-122 NTIS No. PB2001-107277. 52pp.
- Stenson, G. B., Hammill, M. O., Kingsley, M. C. S., Sjare, B., Warren, W. G., and Myers, R. A. (2002). Is there evidence of increased pup production in northwest Atlantic harp seals, *Pagophilus groenlandicus*? *ICES Journal of Marine Science* **10**, 1–12.
- Stenson, G. B., Hammill, M. O., and Lawson, J. W. (1995). Predation of Atlantic cod, Capelin, and Arctic cod by harp seals in Atlantic Canada. *DFO Atlantic Fisheries Research Document* **72**, 1–29.
- Sullivan, C. W., Arrigo, K. R., McClain, C. R., Comiso, J. C., and Firestone, J. (1993). Distributions of phytoplankton blooms in the Southern Ocean. *Science* **262**, 1832–1837.
- Swain, D. P., and Sinclair, A. F. (2000). Pelagic fishes and the cod recruitment dilemma in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Science* **57**, 1321–1325.
- Sydeman, W. J., and Allen S. G. (1999). Pinniped population dynamics in Central California: Correlations with sea surface temperature and upwelling indices. *Marine Mammal Science* **15**, 446–461.
- Tershy, B. R., Breese D., and Alvarez-Borrego S. (1991). Increase in cetacean and seabird numbers in the Canal de Ballenas during an El Niño-Southern Oscillation event. *Marine Ecology Progress Series* **69**, 299–302.
- Testa, J. W. (1987). Long-term reproductive patterns and sighting bias in Weddell seals (*Leptonychotes weddellii*). *Canadian Journal of Zoology* **65**, 1091–1099.
- Testa, J. W. (1990). A comparison of reproductive parameters among three populations of Weddell seals (*Leptonychotes weddellii*). *Journal of Animal Ecology* **59**, 1165–1175.
- Testa, J. W., Oehlert, G., Ainley, D. G., Bengston, J. L., Siniff, D. B., Laws, R. M., and Rounsevell, D. (1991). Temporal variability in Antarctic marine ecosystems: periodic fluctuations in the phocid seals. *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 631–639.
- Thompson, P. M., and Ollason, J. C. (2001). Lagged effects of ocean climate change on fulmar population dynamics. *Nature* **413**, 417–420.
- Thompson, R. B., Butterworth, D. S., Boyd, I. L., and Croxall, J. P. (2000). Modeling the consequences of Antarctic krill harvesting on Antarctic fur seals. *Ecological Applications* **10**, 1806–1819.
- Tierney, M., Hindell, M. A., Lea, M. A., and Tollit, D. (2001). A comparison of techniques used to determine body condition of southern elephant seals, *Mirounga leonina*. *Wildlife Research* **28**, 581–588.
- Tollit, D. J., and Thompson, P. M. (1996). Seasonal and between-year variations in the diet of harbour seals in the Moray Firth, Scotland. *Canadian Journal of Zoology* **74**, 1110–1121.
- Trenberth, K. E. (1990). Recent observed interdecadal climate changes in the northern hemisphere. *Bulletin of the American Meteorological Society* **71**, 988–993.
- Trenberth, K. E., and Hurrell J. W. (1994). Decadal atmosphere-ocean variations in the Pacific. *Climate Dynamics* **9**, 303–319.
- Trillmich, F. (1986). Attendance behavior of Galapagos fur seals. In *Fur seals Maternal strategies on land and at sea*. (Eds R. L. Gentry and G. L. Kooyman.) pp. 168–185. Princeton University Press: Princeton.
- Trillmich, F. (1993). Influence of rare ecological events on pinniped social structure and population dynamics. *Symposia of the Zoological Society of London* **66**, 95–114.
- Trillmich, F., and Limberger D. (1985). Drastic effects of El Niño on Galapagos pinnipeds. *Oecologia* **67**, 19–22.
- Trillmich, F., and Dellinger, T. (1991). The effects of El Niño on Galapagos pinnipeds. In *Pinnipeds and El Niño: Responses to environmental stress*. (Eds F. Trillmich and K. A. Ono). Vol. 88, pp. 66–74. Springer-Verlag, Berlin.
- Trillmich, F., and Ono, K. A. (1991). Pinnipeds and El Niño: Responses to environmental stress. Springer-Verlag, Berlin.
- Trillmich, F., Kooyman, G. L., Majluf, P., and Sanchez-Griñan, M. (1986). Attendance and diving behaviour of South American fur seals during El Niño in 1983. In *Fur seals: maternal strategies on land and at sea*. (Eds R. L. Gentry and G. L. Kooyman.) pp. 153–167. Princeton University Press, Princeton.
- Trites, A. W. (1993). Biased estimates of fur seal pup mass: origins and implications. *Journal of Zoology (London)* **229**, 515–525.
- Trites, A. W., and Bigg M. A. (1996). Physical growth of northern fur seals (*Callorhinus ursinus*): seasonal fluctuations and migratory influences. *Journal of Zoology (London)* **238**, 459–482.
- van den Hoff, J., Burton, H. R., Hindell, M. A., Sumner, M. D., and McMahon, C. R. (2002). Migrations and foraging of juvenile southern elephant seals from Macquarie Island within CCAMLR managed areas. *Antarctic Science* **14**, 134–145.
- Wanless, S., French, D. D., Harris, M. P., and Langslow, D. R. (1982). Detection of changes in the numbers of cliff nesting seabirds in Orkney 1976–1980. *Journal of Animal Ecology* **51**, 785–795.
- White, W. B., and Peterson, R. G. (1996). An Antarctic circumpolar wave in surface pressure, wind, temperature and sea ice extent. *Nature* **380**, 699–702.
- Yodzis, P. (2000). Diffuse effects in food webs. *Ecology* **81**, 261–266.
- Yodzis, P. (2001). Must top predators be culled for the sake of fisheries? *Trends in Ecology and Evolution* **16**, 78–84.
- York, A. E. (1994). The population dynamics of northern sea lions, 1975–1985. *Marine Mammal Science* **10**, 38–51.
- York, A. E., Merrick, R. L., and Loughlin, T. R. (1996). An analysis of the Steller sea lions metapopulation in Alaska. In *Metapopulations and wildlife conservation*. (Ed. D. R. McCullough.) pp. 259–292. Island Press, Washington.
- Young, T. P. (1994). Natural die-offs of large mammals – implications for conservation. *Conservation Biology* **8**, 410–418.