Linking predator foraging behaviour and diet with variability in continental shelf ecosystems: grey seals of eastern Canada

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Upper-trophic-level marine predators are presumed to respond to environmental variability. However, the nature of these responses has been studied in few pinnipeds, particularly during the non-breeding season. Between 1992 and 2003, we measured a suite of behavioural, dietary and life-history variables in grey seals; variables which were expected to vary in response to changes in prey availability. We found significant inter-annual variation in some diving variables indicative of foraging effort and in the species composition of their diets. Postpartum body mass of adult females did not vary inter-annually, but duration of offspring investment (lactation length), total energy investment (offspring weaning mass) and the difference in weaning mass of male and female pups did. There was considerable inter-annual variation in the estimated biomass of grey seal prey species from summer bottom-trawl surveys; however, there was little correlation between grey seal response variables with those estimates. There could be several reasons for this result, but three stand out. First, grey seal numbers on the Scotian Shelf have increased exponentially over the past four decades, implying overall favourable environmental conditions. Grey seals may have adjusted their behaviour and diet to account for variability in prey characteristics other than biomass. Secondly, foraging grey seals and their prey were not sampled at the same time of year. Finally, trends in the biomass of many of the species eaten by grey seals are poorly estimated, thus limiting our understanding of predator responses to ecosystem state.

Ecosystems are complex systems in which interactions among species occur at multiple spatial and temporal scales (Allen 1985, Levin 1992). Sustainable use of marine ecosystems will depend on a better understanding of the mechanisms underlying responses of ecosystems to natural forcing and human impacts. To do this will require a variety of approaches, including process studies and long-term measurements at multiple spatial and temporal scales. For many decades, measurements of lower trophic levels (e.g. zooplankton and fishes) have been used to determine how marine ecosystems change over time (e.g. Mahon *et al.* 1998, Sherman *et al.* 1998). Although upper-trophic-level predators have been monitored as indicators of ecosystem changes in the Southern Ocean for a number of decades (Reid & Croxall 2001, Reid *et al.* (Chapter 17 in this volume), Trathan *et al.* (Chapter 3 in this volume)), and it has been suggested that they may also be useful in other ecosystems (e.g. Montevecchi *et al.* (Chapter 8), Furness (Chapter 14) and Tasker (Chapter 24) in this volume), the value of top marine predators as indicators of ecosystem state has not been widely investigated.

The grey seal (*Halichoerus grypus*) is a size-dimorphic member of the family Phocidae, with males being about 50% heavier than females (McLaren 1993). This species has several attributes that make them potentially useful indicators of ecosystem state. They are large (>100 kg) and long-lived (~40 years) and, thus, individuals must have evolved to cope with variability at various temporal (months to decades) and spatial (<1 km to 1000 km) scales. Most females give birth each year to a single pup, beginning at age 4 or 5 years and continuing for several decades. Female grey seals are capital breeders and females with low body mass at parturition tend to wean smaller pups or wean pups prematurely (Iverson *et al.* 1993, Mellish *et al.* 1999, Pomeroy *et al.* 1999), increasing the probability of juvenile mortality (Coulson 1960, Hall *et al.* 2001). These strong maternal effects on offspring provide a basis for expecting variation in life-history traits in response to environmental variability.

Grey seals are the most abundant pinniped inhabiting the Scotian Shelf and adjacent areas. The number of pups born on Sable Island has increased exponentially for the past four decades, with a doubling time of ~6 years (Bowen *et al.* 2003). Thus, they represent a significant source of predation mortality in fish, particularly during the 1990s. Grey seals disperse widely over the continental shelf of the northwest Atlantic during the non-breeding season (Stobo *et al.* 1990) and are capable of foraging in many habitats throughout this range. They are generalist predators of demersal and pelagic fishes, but typically a small number of prey dominate the

Table 5.1. *Response variables measured in grey seals*

	Variables	Period
Behavioural		
Individual dives	Mean duration, depth, bottom time, % time at depth, % square dives, descent and ascent rates, surface time between dives, number of dives per day, total duration diving per day, total bottom time per day	1992–2001
Dive bouts	Mean duration, depth, % bout at depth, % square dives per bout, % V-shaped dives per bout, number of dives per bout, total time in bout per day	1992–2001
Diet	% species composition, diversity, energy density	1994–2002
Life history		
Maternal	Postpartum body mass, lactation length	1992–2001
Offspring	Weaning body mass, change in male and female weaning mass	1992–2001

diet at any one time or place (Bowen *et al.* 1993, Bowen & Harrison 1994), probably reflecting local prey abundance. Given their broad geographic distribution and their accessibility at the main breeding site on Sable Island, grey seals may provide an opportunity to monitor changes in the Scotian Shelf ecosystem. Here we address two questions: (1) do behavioural, dietary and life-history variables of grey seals vary over time; (2) do these responses correlate with particular features of environmental variability?

DATA COLLECTION

The data were collected from 1992 to 2003 on Sable Island (43° 55′ N, 60° 00′ W), a crescent-shaped, partially vegetated sandbar approximately 300 km southeast of Halifax, Nova Scotia, Canada. Sable Island is the largest haul-out and breeding colony for grey seals in the northwest Atlantic population. Seals congregate on the island in May and June to moult and again in late December and January to rear offspring and mate. Thousands of grey seals also haul out on the island throughout the year between foraging trips. We studied a suite of behavioural, dietary and life-history variables to investigate responses of grey seals to environmental variability (Table 5.1).

DISTRIBUTION

We determined foraging locations of 70 grey seals using satellite-relay data loggers (SRDLs; Wildlife Computers, Redmond, WA, USA or ST-18s; Telonics, Mesa, AZ, USA) fitted to seals in either May/June or
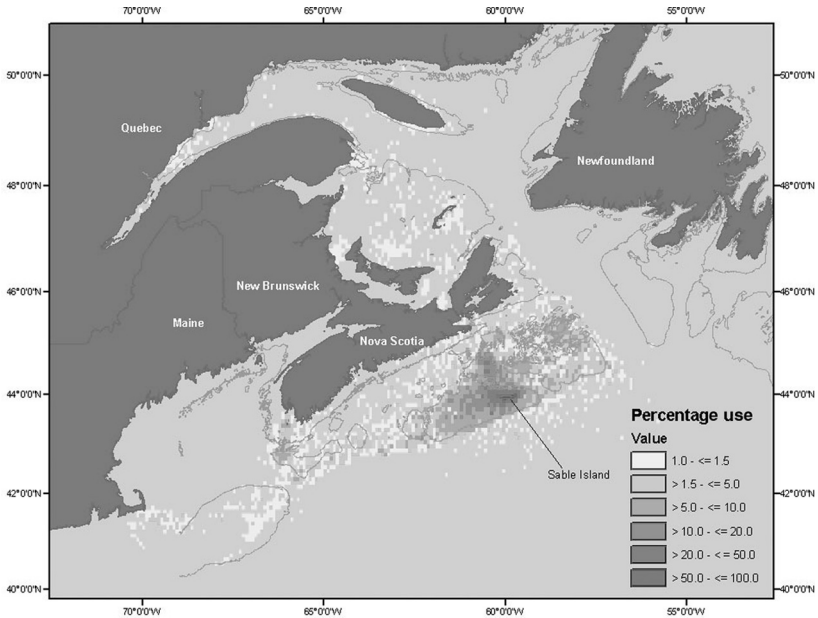
Fig. 5.1   Annual distribution of grey seals based on locations of 70 adults fitted with Argos satellite tags on Sable Island ($n = 18$ for May/June, $n = 38$ for September/October, $n = 14$ for January). To determine the spatial distribution of the population (i.e. percentage usage), we divided the study area into $5' \times 5'$ cells and counted the number of seals that entered each cell. Multiple use of a cell by an individual seal was scored as a single use to avoid biasing the population distribution by the behaviour of individual seals. Too few seals were tagged in each year to permit the analysis of inter-annual changes in the use of space. The 100-m isobath is indicated by a grey line.

September/October from 1995 to 2001 and in January 2003 (described in Austin *et al.* (2004)). Locations were determined from data collected by Service Argos. Locations for each seal (including auxiliary locations) were filtered using a three-stage algorithm (Austin *et al.* 2003) to remove erroneous data.

Most grey seal locations were confined to the continental shelves off eastern Canada and the United States, although transit within and among shelves occasionally occurred over deeper waters (Fig. 5.1). Within this range, the areas <100 m depth were used particularly often. Some offshore banks are clearly delimited by the distribution of locations, with Sable Island, and Western and Middle banks (areas near Sable Island) being used by most seals (Fig. 5.1). This representation presumably provides a reasonable illustration of the spatial scale of the population and foraging areas that
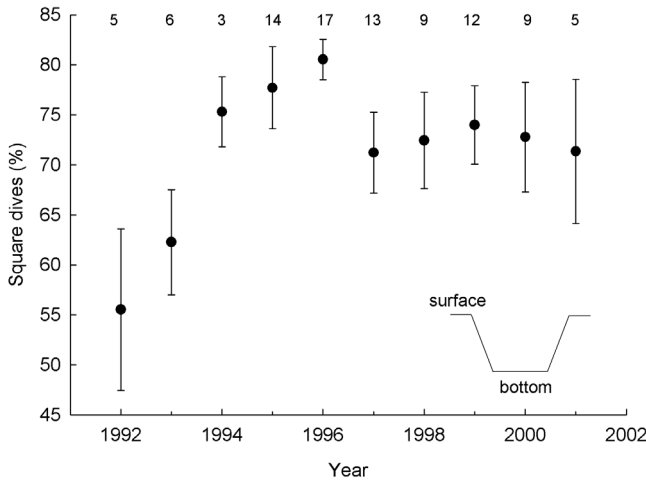
Fig. 5.2   Percentage of square-shaped dives (± 1 SE) used by grey seals between September and December of each year. Number of seals studied is given above the symbol. Percentage of square-shaped dives differed among years (MANOVA: $F_{8,81} = 2.4, p = 0.024$).

probably underlie variation in grey seal response variables. Nevertheless, habitat use by individual seals is highly variable (Austin *et al.* 2004).

RESPONSE VARIABLES

Diving behaviour

We measured characteristics of 8089 ± 403 dives per individual in 93 (46 males and 47 females) adult grey seals over an average of 51 ± 2.5 days during the period from September to December. Using the analytical methods of Beck *et al.* (2003a, 2003b), we found that diving behaviour showed significant inter-annual variability at the scale of individual dives (MANOVA: year – $F_{63, 511} = 1.38, p = 0.035$). Although depth, duration, and descent and ascent rates of individual dives did not vary inter-annually, surface time between dives did (1994 excluded because of small sample size; $F_{8,81} = 2.5, p = 0.016$), with surface intervals being significantly shorter in 1993 compared with other years. The percentage of square-shaped dives also differed significantly among years (Fig. 5.2). Inter-annual variation was also evident in bout characteristics (MANOVA: year – $F_{45, 340} = 1.72, p = 0.004$), with an increasing linear trend in the percentage of bouts spent at depth ($F_{7,83} = 2.2, p = 0.04$).
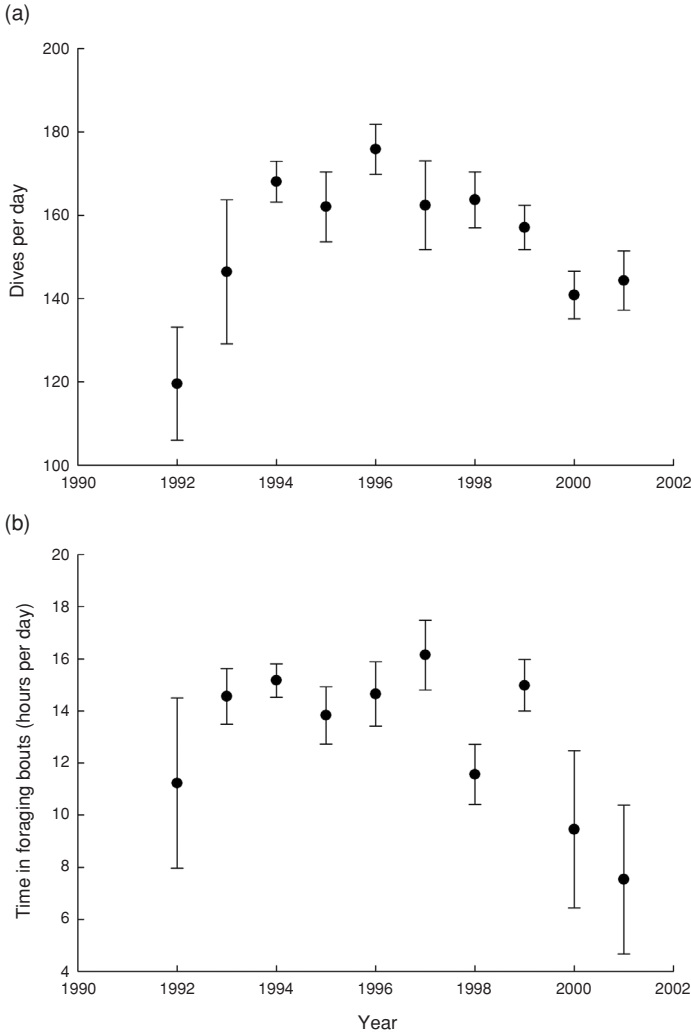
(a)

(b)

Fig. 5.3   Inter-annual indices of foraging effort (± 1 SE) (a) Mean number of dives per day. (b) Time spent in foraging bouts. Sample sizes are as given in Fig. 5.2. Based on MANOVA, both indices varied inter-annually: dives per day, $F_{8,81} = 2.9$ and $p = 0.007$; hours in foraging bouts, $F_{7,74} = 2.7$ and $p = 0.014$.

Two of the three indices (number of dives per day, time spent in foraging bouts and time spent at depth) of foraging effort varied significantly among years. Dives per day increased through the mid 1990s and declined through the late 1990s into 2001 (Fig. 5.3a). Hours spent in foraging bouts was relatively stable from 1992 to 1997, then declined significantly in

1998 only to increase to former levels in 1999, and subsequently decline (Fig. 5.3b). Number of dives per day was positively correlated with the proportion of square dives exhibited each year ($r = 0.85$, $p = 0.002$).

Diet

We used quantitative fatty acid signature analysis (QFASA; Iverson *et al.*, 2004 (Chapter 7 in this volume)) to derive estimates of diet using a prey fatty acid library of 27 species of fish and invertebrates collected from the study area. Blubber biopsies were collected from the posterior flank of seals shortly after they arrived on the breeding colony in January 1994 through 2002. Individual adult grey seals consumed between 1 and 10 prey species in the 4 months prior to arriving at the breeding colony, averaging 4.3 ± 0.11 prey species per individual. Diet diversity varied significantly among years (Fig. 5.4a). However, despite this variation, energy density (kJ g^{-1}) of the diet did not vary among years (ANOVA: $F_{8,\,322} = 0.84$, $p = 0.57$; average 5.5 ± 0.02 kJ g^{-1}; range 4.6–6.6 kJ g^{-1}).

Species composition of the diet also varied significantly among years (Fig. 5.4b). In each year, two to five species accounted for over 80% of the diet by weight, with northern sand lance (*Ammodytes dubius*) and redfish (*Sebastes* spp.) dominating the diet. The proportions of nine different prey species – including cod (*Gadus morhua*), gaspereau (*Alosa pseudoharengus*), squid (*Illex illecebrosus*) and thorny skate (*Raja radiata*) – differed significantly among years. However, it was the proportions of pollock (*Pollachius virens*), redfish, sand lance, witch flounder (*Glyptocephalus cynoglossus*), and winter skate (*Raja ocellata*) that exhibited the greatest inter-annual variability in the diet. Pollock was significantly more abundant in the diet in 1994, 1998 and 2000–2001 than in other years. Sand lance accounted for significantly less of the diet in 1994 and 1998 than in other years, whereas redfish made up a particularly small proportion of the diet in 2000. Several other demersal fishes also contributed more to the diet in 1994, 1998 (witch flounder) and 2000 (winter skate *Raja radiata*) compared with other years.

We hypothesized that grey seal diving behaviour might vary with the ratio of the dominant prey types in the diet, as these prey species differ in many characteristics. We found a positive correlation between the ratio of redfish to sand lance in the diet and the number of dives per day ($r = 0.71$, $n = 9$, $p = 0.03$), but no significant correlation with the proportion of square-shaped dives ($p = 0.61$) or total time spent in diving bouts ($p = 0.13$).
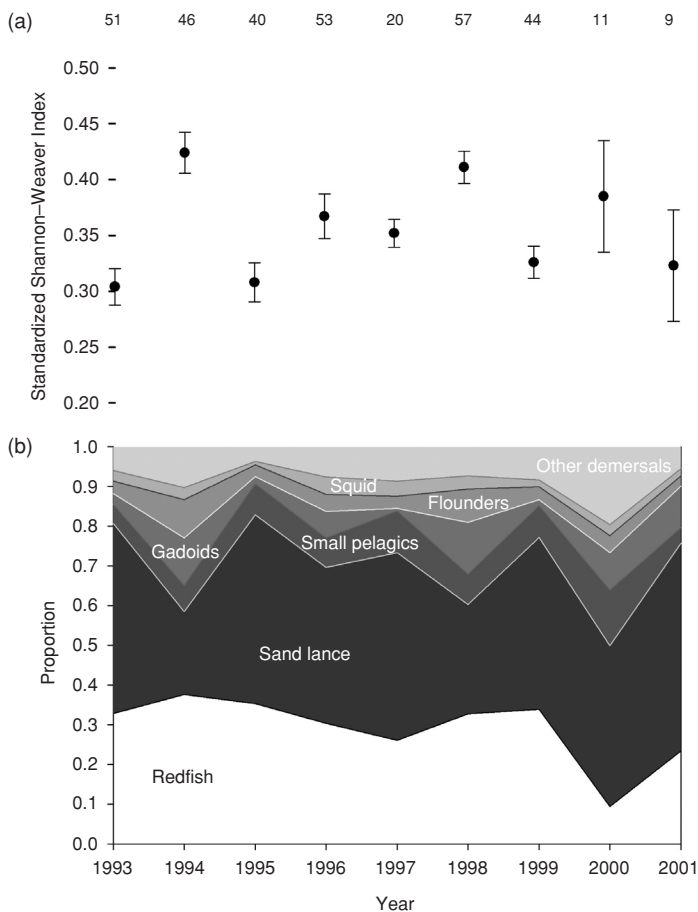
Fig. 5.4   (a) Inter-annual estimates of Shannon–Weaver standardized index (range 0 to 1) of diet diversity (± 1 SE). Diet diversity varied among years (ANOVA: $F_{8,322} = 5.1$, $p < 0.001$): 1994 differed from 1993, 1995 and 1999; 1995 differed from 1998; 1998 differed from 1999. Diet estimates were based on fatty acids extracted from blubber cores using the methods of Iverson *et al.* (2001). Fatty acid composition was analysed according to Iverson *et al.* (2002) and Budge *et al.* (2002) and used to estimate diet composition following Iverson *et al.* (2004, Chapter 7 in this volume). The number of seals studied is given above the symbols. (b) Percentage contribution of prey species to the diet of grey seals differed significantly among years ($p = 0.0001$): 1993 differed from 1994 and 1998; 1994 differed from 1995–7 and 1999–2000; 1995 differed from 1998 and 2000; 1996 differed from 1998; 1997 differed from 1998 and 2000; 1998 differed from 1999 and 2000. Inter-annual variability in diet was tested using permutation tests. The Kulback–Liebler distances among the mean diet composition for each year were calculated and then the diet estimates of individuals were randomly assigned 10 000 times each year. Then the mean diet composition for each year and the distance between the new yearly means again was computed creating a distribution against which to test the observed distance. A Bonferroni correction was applied to the resulting *p* values to account for the multiple comparisons. Sample sizes are as in Fig. 5.4a.

Life history

Variability in food availability might be reflected in the body mass of females arriving at the breeding colony to give birth. In turn, inter-annual variability in maternal postpartum mass (MPPM) might affect the duration of energy investment (lactation length) and the allocation of energy to offspring (pup weaning mass). Thus, each year we weighed a sample of known-age females at 3 days postpartum and determined lactation length and weaning date based on daily surveys throughout the colony.

MPPM did not differ significantly among years (Fig. 5.5a). Lactation length in grey seals exhibited significant quadratic variation with maternal age (W. D. Bowen, unpublished observations). Thus, inter-annual estimates of lactation length were adjusted to account for differences in the mean age of females sampled among years. When this was done there was a significant difference in mean lactation length among years (Fig. 5.5b) with 1993–5 having shorter lactation periods than other years. However, year accounted for only 2.4% of the variation and therefore is of doubtful biological significance. As with lactation length, weaning mass also varied in a quadratic manner with maternal age. Mean weaning mass (corrected for maternal age) varied significantly among years (Fig. 5.5c). Weaning mass in 1998 was significantly greater than in 2000, but there were no other significant differences among years.

Male pups are heavier than female pups, and therefore require a greater absolute energy investment by mothers. Thus, variation in the average difference in the weaning mass of male and female pups may indicate years in which adult females were in relatively better condition, having stored more energy prior to arrival at the breeding colony. We calculated the difference between male and female weaning masses each year, corrected for the effect of maternal age on weaning mass. Differences between the mean weaning mass of male and female pups were larger than average in 1993, 1998 and 2002 (Fig. 5.6). However, the interpretation of these findings is not clear as other life-history measures did not indicate that females were in better condition or made greater overall energy investment in their offspring in those years.

ENVIRONMENTAL VARIABILITY

Environmental variability on the Scotian Shelf, the marine ecosystem primarily used by grey seals from Sable Island, is summarized in Zwanenburg *et al.* (2002). Inter-annual changes in water temperatures and salinities on
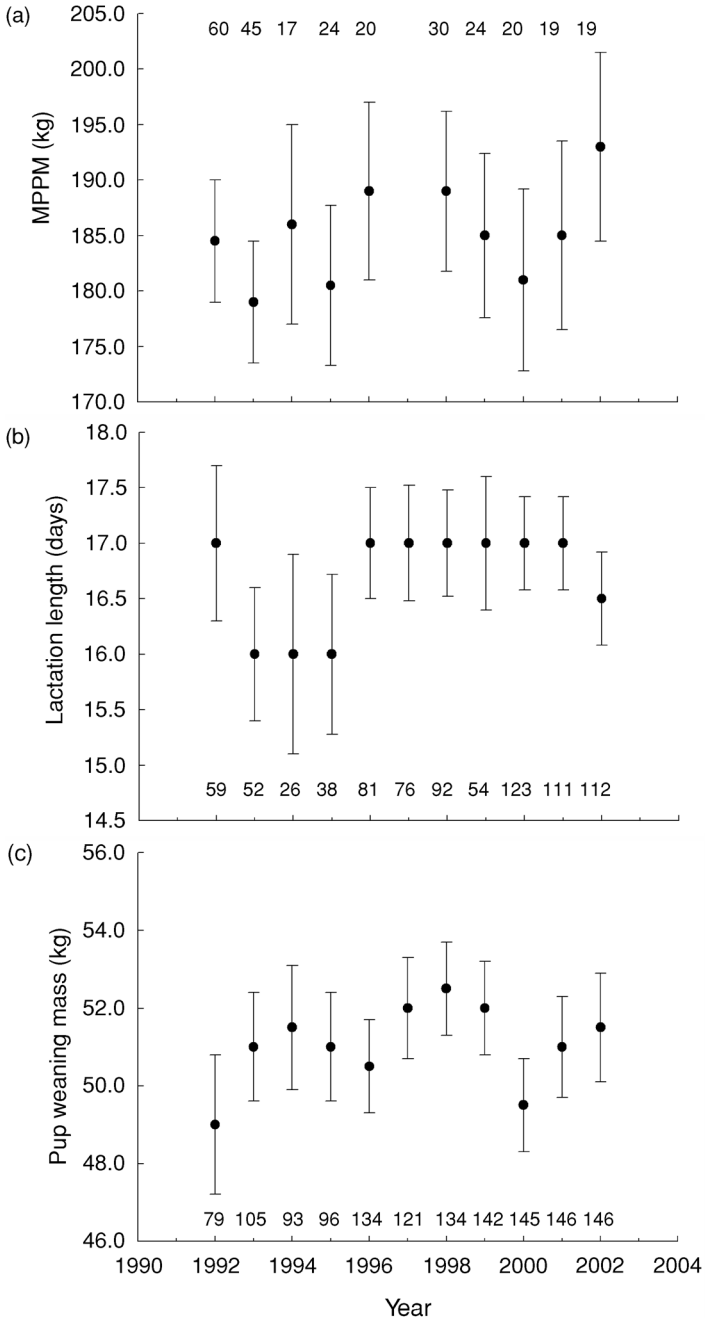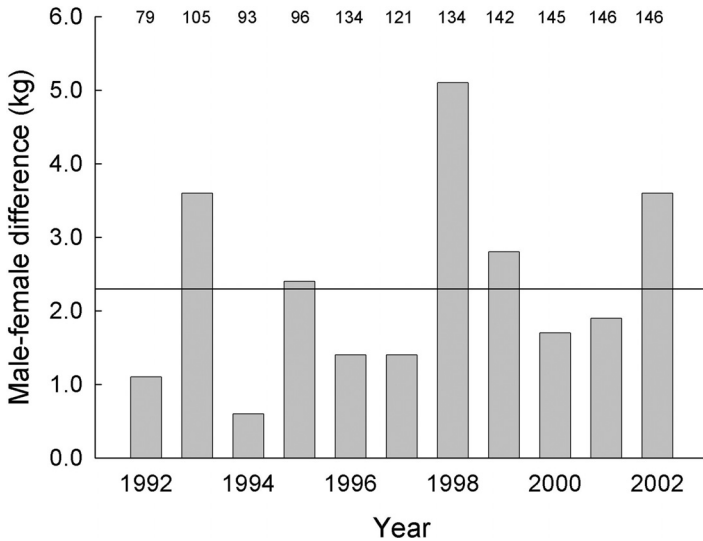
Fig. 5.6   Inter-annual estimates of the difference in mean weaning mass of male and female grey seal pups.

the Scotian Shelf are among the most variable in the North Atlantic. On the northeastern Scotian Shelf the cold, intermediate-layer water, represented by Misaine Bank at 100 m depth, fell sharply by the mid 1980s and remained below normal through 1995, returning to the climatological mean in the period 1997 to 2002 (DFO 2003). Despite these changes, the estimated mean composition of the winter grey seal diet was similar during the cold period and during years when temperature had returned to average conditions (MANOVA: $F_{8,322} = 1.8$, $p = 0.09$; Table 5.2).

There were large inter-annual changes in the estimated biomass of some prey species during the 1990s (Fig. 5.7). However, to a considerable degree the magnitude of those changes are more difficult to assess as the bottom-trawl inconsistently samples species such as redfish, sand lance, capelin and

Fig. 5.5   Inter-annual estimates of: (a) maternal postpartum mass (MPPM), (b) lactation length and (c) pup weaning mass of grey seals. Estimated means of MPPM did not differ among years (univariate general linear model (GLM) with maternal age as a covariate, $F_{9, 267} = 1.4$, $p = 0.21$); estimated mean lactation length among years (adjusted for differences in mean maternal age) differed inter-annually (univariate GLM with maternal age and maternal age 5 squared as covariates, $F_{10, 811} = 2.0$, $p = 0.03$); estimated mean weaning mass varied among years (univariate GLM with maternal age and maternal age 5 squared as covariates, $F_{10, 1328} = 2.4$, $p = 0.01$). Error bars are 95% confidence limits.

Table 5.2. *Percentage composition of grey seal diets during a cold-water period (1993–6) and after a return to climatological average temperatures (1997–2001) based on average annual water temperature at 100 m, Misaine Bank*

Species	Period	
	Cold	Average
Redfish	33.8	29.7
Sand lance	38.8	37.8
Other forage fish[a]	6.6	8.4
Cod	1.8	1.0
Other demersals[b]	6.8	8.4
Flounders[c]	5.0	5.3
Skates[d]	4.3	6.6
Squid	2.9	2.7

[a]Capelin (*Mallotus villosus*), herring (*Clupea harengus*), mackerel (*Scomber scombrus*), snakeblenny (*Lumpenus lumpretaeformis*), gaspereau (*Alosa pseudoharengus*).
[b]Pollock, haddock (*Melanogrammus aeglefinus*), lumpfish (*Cyclopterus lumpus*).
[c]American plaice (*Hippoglossoides platessoides*), yellowtail (*Limanda ferruginea*), witch flounder, winter flounder, turbot (*Rheinhardtius hippoglossoides*).
[d]Thorny skate (*Raja radiata*), winter skate (*Raja ocellata*).

pollock. This inconsistent sampling is suggested by the dramatic apparent increase in capelin biomass in 1994 and pollock biomass in 1996 (Fig. 5.7). These are some of the more frequently consumed grey seal prey, thus making it difficult to determine how grey seal consumption may respond to prey abundance. Nevertheless, the abundance of sand lance clearly increased over the course of our study, whereas capelin decreased and redfish biomass seems to have been relatively stable (Fig. 5.7). Flounders also appeared to have increased during the later part of our study, whereas pollock biomass fluctuated, but in general declined. Despite inter-annual variation in both estimated diet and prey abundance, the proportions of the dominant prey (i.e. redfish, sand lance, pollock) in the diet were not significantly correlated with prey abundance.

SEALS AS INDICATORS OF ECOSYSTEM STATE

The idea that upper-trophic-level predators can provide information that could be used to improve the management of marine species is attractive because such predators sample their environment at a range of spatial and temporal scales that are difficult and expensive to achieve using research
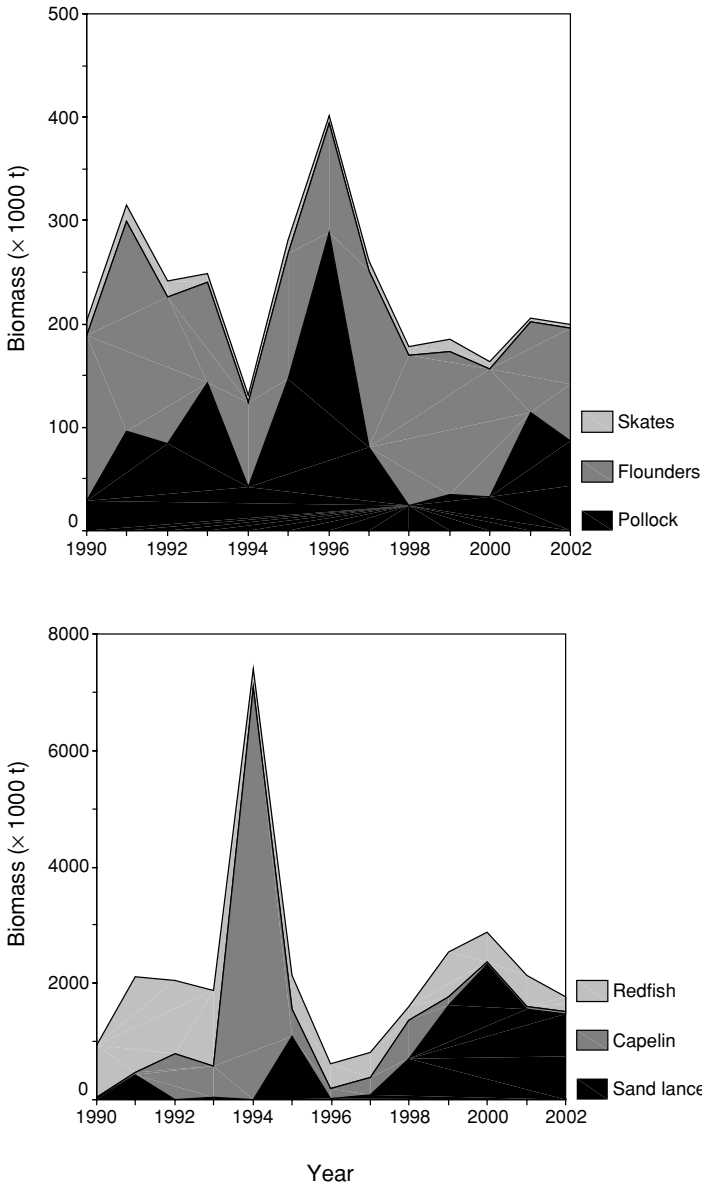
Fig. 5.7 Biomass estimates of selected grey seal prey from July bottom-trawl surveys, 1990–2002. Inter-annual variability in fish abundance was derived from synoptic, stratified-random, bottom-trawl surveys conducted each July. Estimates of species biomass, corrected for catchability to provide a better indication of true relative abundance, were combined for the trawl survey strata primarily used by grey seals. However, species such as sand lance, redfish, capelin and pollock are poorly sampled by bottom trawls such that the resulting biomass estimates are biased and observed trends may provide only a rough indication of true trends.

and commercial vessels. Nevertheless, the use of predators for this purpose requires an understanding of how predator responses are linked to the variability in particular ecosystem components (Croxall *et al.* 1988, Boyd & Murray 2001, Hindell *et al.* 2003). We found significant inter-annual variation in aspects of foraging behaviour, diet and several life-history variables of grey seals over the 10 years of our study. Presumably, differences in foraging behaviour and diet are causal, reflecting the need to use different foraging tactics to locate and capture different prey species (e.g. redfish versus sand lance) (Bowen *et al.* 2002). Similarly, differences in behaviour and diet are presumably related to changes in the availability of prey. However, the links among these variables are not clear in our data.

The continental-shelf ecosystems inhabited by grey seals in eastern Canada have exhibited considerable variability over the past several decades – involving changes in physical and biological oceanography, fisheries exploitation rates and species abundance – with a general shift from a system dominated by demersal fishes to one dominated by pelagic fish species (Rice 2000, Swain & Sinclair 2000, Zwanenburg *et al.* 2002). Thus, there were considerable changes in ecosystem state to test whether grey seals revealed those changes. However, only grey seal pup production at Sable Island was monitored over those earlier several decades. Measurements of the behavioural, diet and life-history variables were only initiated in the early 1990s after many of the larger changes had already occurred.

Grey seals are large, long-lived mammals with K-selected life histories. Despite the large environmental changes observed over the past four decades on the Scotian Shelf (Zwanenburg *et al.* 2002), the grey seal population size has increased steadily from only a few thousand seals in the 1960s to about 175 000 in 1995 (Mohn & Bowen 1996). Pup production on Sable Island increased exponentially, at a rate near the maximum possible (r_{max}), through the late 1990s (Bowen *et al.* 2003). Although there is no a-priori reason to have expected exponential population growth, the fact that it occurred suggests that – from a grey seal perspective – the environment was favourable throughout this period. This demographic history provides an essential context for interpreting the performance of the response variables measured in this study.

Diving behaviour ought to reflect characteristics of the prey available to pinnipeds since all foraging necessarily occurs during diving. The relationship between diving behaviour and changes in prey availability is perhaps best understood in Antarctic fur seals (*Arctocephalus gazella*) (e.g. Bengtson 1988, Boyd *et al.* 1994, McCafferty *et al.* 1998). Females in this species altered both trip duration and number of dives in response to changes in

krill abundance and the amount of fish and squid in the diet. However, these conclusions are limited to the period of offspring provisioning and thus may not be representative of responses at other times of the year, or in males. We studied diving behaviour of adult male and female grey seals over the 4 months prior to arrival at the breeding colony. During this period both sexes gain mass (Beck *et al.* 2003c), indicating that this is a period of heavy feeding. Although most variables describing individual dives or bouts of dives exhibited little inter-annual variability, number of dives per day, proportion of square-shaped dives, proportion of dive bout spent at depth and total time spent in diving bouts per day varied among years. However, for the most part, inter-annual variation in foraging behaviour was not related to differences in diet or estimated prey biomass. Number of dives per day was positively correlated with the ratio of the two dominant prey in the diet, redfish and sand lance. However, this finding is difficult to interpret without knowing how predator foraging tactics differ for these prey types.

Inter-annual variation in pinniped diets is generally assumed to reflect changes in prey abundance and encounter rates (Bowen & Siniff 1999). Although demersal species accounted for ~25% of the grey seal diet in some years, diets were dominated by sand lance and redfish. The percentage of those two species in the diet varied significantly among years. However, there was no correlation between this variation and estimates of prey biomass from trawl surveys conducted within grey seal habitat. There are a number of possible reasons for this. Firstly, the estimate of prey biomass was derived from the survey conducted in July, whereas our diet samples were collected about 5 months after the survey. Although fatty-acid-based estimates of diet should integrate intake over several months (Iverson *et al.* 2004), both prey availability and grey seal distribution are presumably dynamic such that the July survey may not be a good measure of prey available to seals months later. Secondly, the trawl survey is known to sample both redfish and sand lance inconsistently. Thus, the true abundance of these species may not be reflected by the survey. Thirdly, the small number of grey seals sampled in some years (e.g. 1997, 2000 and 2001) may not have been representative of grey seal diets. Obtaining a representative sample may be difficult for a wide-ranging predator exploiting a spatially heterogeneous habitat. Fourthly, although we know little about the ontogeny of foraging behaviour in grey seals and other pinnipeds, it is reasonable to expect that learning plays an important role in the diet of individual seals resulting in strong individual differences in diet among individuals foraging in the same habitat (Estes *et al.* 2003). Individual prey preferences may partially obscure responses at the population level, particularly when

overall prey resources are not limited. Finally, and perhaps most importantly, given the favourable prey environment (as judged by the rapid rate of population increase), it is possible that grey seals were foraging in the range of the asymptotic limb of the non-linear functional response curve (Furness (Chapter 14 in this volume)) where consumption is relatively insensitive to changes in prey biomass. If true, the interpretation of predator responses will be contingent on demography.

The significance of changes in foraging behaviour and diet to the predator can only be determined through their effects on demography (Croxall *et al.* 1988). However, annual estimates of survival and fecundity are difficult to measure in most pinnipeds. Maternal and offspring size and condition are attractive because they can be easily measured, ought to reflect changes in prey availability and can affect demography. We found that MPPM, an index of foraging success, did not vary among years. Duration of maternal investment (i.e. lactation length) and pup weaning mass exhibited significant, but relatively little, inter-annual variation. Interestingly, in the year (1998) that the difference between male and female weaning mass was greatest, combined pup weaning mass was also the highest, perhaps suggesting that adult females were in particularly good condition that year. However, in general, these life-history response variables in grey seals were not informative of ecosystem state. As noted above, our data were collected during a period when this population was experiencing favourable environmental conditions and exponential population growth. The same variables measured during a period of population decline or stability may have responded quite differently.

For the present, we conclude that despite the large changes in estimates of invertebrate- and fish-species abundances (Zwanenburg *et al.* 2002), MPPM, lactation length and offspring weaning mass provided little indication of those environmental changes. Although we observed greater inter-annual variability in the foraging behaviour and diet, those response variables for the most part were also not informative with respect to specific ecosystem changes that occurred during the 1990s. However, we believe it would be premature to suggest that grey seals and similar species will not be useful monitors on the basis of this initial exploratory analysis. It is possible that grey seal diets are better indicators of abundance for many of the species consumed than are the bottom-trawl surveys routinely used for this purpose. Comparison of species estimates in the diet of grey seal against reconstructed prey-population abundance from catch-at-age models might provide a means of validating this hypothesis. Measurement of foraging behaviour and diet response variables at other times of the year may

be more informative because they coincide more closely with measures of prey distribution and abundance from surveys. Combining information on the spatial distribution of foraging with diving variables and diet may be a more sensitive indicator of response by grey seals to prey abundance (Boyd *et al.*2002). Finally, the exponential growth observed in this population over the past four decades cannot persist indefinitely. As indicated by fur seal responses to krill abundance (Boyd *et al.* 1994) and the wealth of data on seabirds (e.g. Montevecchi 1993), we expect that many of the response variables examined here will provide more information about ecosystem state when the grey seal population is eventually limited by its food supply.

ACKNOWLEDGEMENTS

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