



## Junk-food in marine ecosystems

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The abundance and availability of food are critical determinants of reproductive success and population dynamics of marine top predators. However, recent work has indicated that the quality of the food may also be critically important for some marine predators. The 'junkfood hypothesis' was originally suggested as a potential explanation for a dramatic population decline of Stellers sea lions *Eumetopias jubatus* in the Gulf of Alaska. According to the hypothesis, a dietary switch to prey of low energy content led to detrimental effects on the population of sea lions. A number of observations indicate that the hypothesis is relevant for several population parameters. Recent work on piscivorous seabirds has provided substantial evidence indicating the relevance of this hypothesis in food webs in e.g. the North Pacific, the North Sea and the Baltic Sea. The emergence of 'junk-food' in these systems may be coupled to large scale changes in climatological and oceanographic forcing, although predation, fishing and competition provide additional plausible hypotheses. It may be possible to predict which kinds of animals will be particularly sensitive to food quality; these seem to be species with limited ability to carry food loads, with energetically-expensive foraging behaviour, and with digestive anatomy evolved to minimize mass at the cost of digestive efficiency. This review suggests that the junk-food hypothesis is a highly relevant factor in relation to sustaining ecosystem resilience, and is an important consideration in ecosystem management. Sustaining healthy populations of marine top-predators requires an understanding of the role of food quality, in addition to food abundance and availability.

### Management of marine food webs in an ecosystem context

Management of marine resources involves a large degree of uncertainty. The accuracy of fish stock assessments is regularly questioned and the relative role of top-down (consumer effects on resources) and bottom-up (resource effects on consumers) forcing for the dynamics of complex marine ecosystems has long been debated (Becker and Beissinger 2006, Halpern et al. 2006, Frederiksen et al. 2007). As fisheries biologists and marine ecologists are increasingly collaborating, interesting dynamics in the web of complex interactions in which fisheries are managed, are becoming apparent (Hughes et al. 2005). Ecological regime shifts (Scheffer et al. 2001, Hunt and Stabeno 2002, Scheffer and Carpenter 2003), with alternate stable states between them have recently been documented in a range of coastal and marine ecosystems, clearly indicating that managers are forced to deal with surprising and rapid changes (Hughes et al. 2005, Hedd et al. 2006, Hunt and McKinnell 2006). Although the dynamics in marine ecosystems can be very similar to those observed in lakes (Scheffer et al. 2005), a substantial difference between lakes and marine ecosystems is the geographical scale of the impacts that changes in fish stocks in the oceans can have on other components of the ecosystem.

Marine fish-eating seabirds and mammals can be substantial consumers of marine resources and are at times regarded as potential competitors with the commercial fishery (Yodzis 2000, Brooke 2004, Karpouzi et al. 2007). These species are commonly charismatic top-predators, and hence important on the conservation agenda. Some of these species have life-styles that expend energy rapidly so require a high rate of energy gain from foraging (Benoit-Bird 2004), and these species may be particularly dependent on high densities of energy-rich prey. A suite of studies has correlated population parameters of marine top predators with the abundance and availability of food (Aebischer et al. 1990, Boyd and Murray 2001, Oro and Furness 2002, Furness 2003, Trites and Donnelly 2003, Bunce et al. 2005, Wanless et al. 2007) and we present some illustrative examples of this in Table 1 (and Fig. 1). In long-lived animals such as seabirds and marine mammals, even a small reduction in adult survival greatly reduces lifetime reproductive success. Therefore, life history theory predicts that under adverse environmental conditions such as scarcity of food, top predators would not increase breeding effort to compensate for food shortage if that would reduce their body condition to levels that would jeopardize survival (Cairns 1987). A corollary of this is that growth of seabird chicks or breeding success of seabirds would be likely to show much greater variation in relation to food than would

Table 1. Published field observations with statistically significant relationships between changes in marine predator life-history parameters and changes in prey abundance or quality (including independent data on predator and prey). The corresponding Latin species names for predators are: a = *Pelecanus occidentalis californicus*, b = *Sterna paradisea*, c = *Larus occidentalis*, d = *Uria aalge*, e = *Spheniscus demersus*, f = *Morus capensis*, g = *Phalacrocorax capensis*, h = *Sterna bergii*, i = *Rissa tridactyla*, j = *Phalacrocorax aristotelis*, k = *Larus audouinii*, l = *Stercorarius parasiticus*, m = *Fratercula arctica*, n = *Diomedea chrysostoma*, o = *Diomedea melanophris*, p = *Pygoscelis papua*, q = *Eudyptes chrysolophus*, r = *Arctocephalus gazella*, s = *Balaenoptera acutorostrata*, t = *Stercorarius skua*, u = *Ptychorampus aleuticus*, v = *Phalacrocorax bougainvillii*, w = *Sula variegata*, x = *Pelecanus thagus*, y = *Otaria flavescens*, z = *Morus serrator*, aa = *Uria lomvia*, ab = *Alca torda*, ac = *Pygoscelis Antarctica*, ad = *Puffinus mauretanicus*, ae = *Brachyrhamphus marmoratus*, af = *Phocoena phocoena*, ag = *Cephus columba*, ah = *Cerorhinca monocerata* and for prey species: I = *Engraulis mordax*, II, *Ammodytes marinus*, III = *Sebastes jordani*, IV = *Engraulis capensis*, V = *Mallotus villosus*, VI = *Clupea harengus*, VII = *Eupuasias superba*, VIII = *Euphausia pacifica*/ *Thysanoessa spinifera*, IX = *Engraulis ringens*, X = *Sardinops sagax*, XI = *Gadus morhua*, XII = *Ammodytes* sp., XIII = *Engraulis encrasicolus*, XIV = *Clupea pallasii*, XV = *Ammodytes hexapterus*, XVI = *Sprattus sprattus*, XVII = *Thysanoessa spinifera*/ *Euphausia pacifica*, XVIII = *Sebastes* spp., XIX = *Cololabis saira*.

| Reference  | Predator   | Prey                               | Region                         | Life-history parameter  | Analysis   |
|--|--|------------------------------------|--------------------------------|---|--|
| <b>Food abundance</b>                            |  |                                    |                                |   |  |
| Anderson et al. 1982                             | Brown pelican <sup>a</sup>   | Northern anchovy <sup>I</sup>      | California current (south)     | Breeding success  | Positive correlation 1970–1979   |
| Monaghan et al. 1989, Suddaby and Ratcliffe 1997 | Arctic tern <sup>b</sup>   | Lesser sandeel <sup>II</sup>       | North Sea (Shetland)           | Breeding success  | Positive (non-linear) relationship 1979–1994   |
| Sydean et al. 1991                               | Western gull <sup>c</sup>  | Shortbelly rockfish <sup>III</sup> | California current             | Breeding success  | Positive correlation 1983–1989   |
| Uttley et al. 1994                               | Common guillemot <sup>d</sup>  | Lesser sandeel <sup>II</sup>       | North Sea (Shetland)           | Chick feeding/weight, fledging success, Adult time budget   | Two years (1990–1991) 40-fold change in sandeel abundance between years  |
| Crawford and Dyer 1995                           | African penguin <sup>e</sup> , Cape gannet <sup>f</sup> , Cape cormorant <sup>g</sup> , swift tern <sup>h</sup>                          | Cape anchovy <sup>IV</sup>         | Benguela current               | Breeding numbers and breeding success   | Positive correlations 1984–1992  |
| Barrett and Krasnov 1996                         | Black-legged kittiwake <sup>i</sup>  | Capelin <sup>V</sup>               | Barents Sea                    | Clutch size   | T-test, prey absent/present 12 years   |
| Monaghan 1996                                    | Arctic tern <sup>b</sup> , black-legged kittiwake <sup>i</sup> , common guillemot <sup>d</sup> , European shag <sup>j</sup>              | Lesser sandeel <sup>II</sup>       | North Sea (Shetland)           | Breeding success and foraging effort  | Positive relationships some variables 1990–1993  |
| Oro et al. 1996                                  | Audouin's gull <sup>k</sup>  | Trawling discards                  | Mediterranean Sea              | Chick growth and breeding success   | Positive relationship  |
| Phillips et al. 1996 (updated)                   | Arctic skua <sup>l</sup>   | Lesser sandeel <sup>II</sup>       | North Sea (Shetland)           | Breeding success  | Positive correlation 1975–2005   |
| Anker-Nilssen et al. 1997                        | Black-legged kittiwake <sup>i</sup>  | Atlantic herring <sup>VI</sup>     | Barents /Norwegian seas        | Fledging success  | Positive correlation 1975–1996   |
| Anker-Nilssen et al. 1997                        | Atlantic puffin <sup>m</sup>   | Atlantic herring <sup>VI</sup>     | Barents /Norwegian seas        | Breeding success  | Positive correlation 1980–1996   |
| Regehr and Montevecchi 1997                      | Black-legged kittiwake <sup>i</sup> and <i>Larus</i> gulls   | Capelin <sup>V</sup>               | Newfoundland-Labrador Shelf    | Proportion of pairs laying eggs, egg and clutch size and breeding success                           | Positive correlations  |
| Croxall et al. 1999                              | Grey-headed albatross <sup>n</sup> , black-browed albatross <sup>o</sup> , gentoo penguin <sup>p</sup> and macaroni penguin <sup>q</sup> | Antarctic krill <sup>VII</sup>     | Southern Ocean (South Georgia) | Fledgling mass and breeding success   | Positive correlations  |
| Furness and Tasker 2000                          | 14 species of seabirds   | Lesser sandeel <sup>II</sup>       | North Sea (Shetland)           | Breeding success  | Reductions during years of low sandeel abundance, pronounced in some species, weak in others, depending on species' ecology. |
| Rindorf et al. 2000                              | Common guillemot <sup>d</sup> , black-legged kittiwake <sup>i</sup> , European shag <sup>j</sup>   | Lesser sandeel <sup>II</sup>       | North Sea (Isle of May)        | Breeding success  | Positive correlations with index of availability of 1 + sandeels   |
| Boyd and Murray 2001                             | Fur seal <sup>r</sup> , macaroni <sup>q</sup> and gentoo penguin <sup>p</sup>  | Antarctic krill <sup>VII</sup>     | Southern Ocean (South Georgia) | Standardized index for 27 variables (e.g. population size, breeding success, offspring growth rate) | Positive non-linear relationship 1977–1998   |
| Haug et al. 2002                                 | Minke whale <sup>s</sup>   | Capelin <sup>V</sup>               | Barents Sea                    | Body condition  | Positive relationship high/low prey abundance 1993–1999  |

Table 1 (Continued)

| Reference  | Predator  | Prey   | Region                         | Life-history parameter  | Analysis  |
|--|---|--|--------------------------------|---|---|
| Oro and Furness 2002                               | Black-legged kittiwake <sup>i</sup> and great skua <sup>t</sup>   | Lesser sandeel <sup>ll</sup>   | North Sea (Shetland)           | Adult survival, breeding success                                | Positive correlation 1986–1997  |
| Abraham and Sydeman 2004                           | Cassin's auklet <sup>u</sup>  | Euphausiids <sup>viii</sup>  | California current             | Meal mass/fledging success                                      | Positive correlations 1975–2001   |
| Frederiksen et al. 2004                            | Black-legged kittiwake <sup>i</sup>   | Lesser sandeel <sup>ll</sup>   | North Sea (Isle of May)        | Breeding success and adult survival                             | Positive correlations   |
| Jahncke et al. 2004                                | Cormoran <sup>v</sup> , booby <sup>w</sup> , pelican <sup>x</sup>   | Peruvian anchovy <sup>ix</sup>   | Peruvian upwelling zone        | Population size   | Positive correlations   |
| Soto et al. 2004                                   | South American sea lion <sup>y</sup>  | Peruvian anchovy <sup>ix</sup>   | Peruvian upwelling zone        | Birth rate  | Positive correlation 1997–2002  |
| Bunce et al. 2005                                  | Australasian gannet <sup>z</sup>  | Pilchard <sup>x</sup>  | Southeast Australian shelf     | Breeding success  | Significantly lower in poor food years 1997–1999  |
| Frederiksen et al. 2005                            | Black-legged kittiwake <sup>i</sup>   | Lesser sandeel <sup>ll</sup>   | North Sea                      | Breeding success  | Positive correlations with local stocks of sandeels and with closely neighbouring colonies of kittiwake |
| Reid et al. 2005                                   | Antarctic fur seal <sup>r</sup> , black-browed albatross <sup>o</sup> , macaroni <sup>l</sup> - and gentoo <sup>p</sup> penguin                         | Antarctic krill <sup>vii</sup>   | Southern Ocean (South Georgia) | Adult/offspring condition, breeding success, population numbers | Positive correlations for some variables 1973–2002  |
| Sandvik et al. 2005                                | Atlantic puffin <sup>m</sup> , black-legged kittiwake <sup>i</sup> , Brünnich <sup>aa</sup> and common guillemot <sup>d</sup> , razorbill <sup>ab</sup> | Cod <sup>xi</sup> , Capelin <sup>v</sup> and Atlantic herring <sup>vi</sup>              | Barents Sea                    | Adult survival  | Positive correlations for some variables 1990–2003  |
| Velando et al. 2005                                | European shag <sup>i</sup>  | Sandeels <sup>xii</sup>  | Iberian coastal ecosystem      | Chick condition, Breeding success                               | Strong reduction in 2003 when sandeel availability low after oil-spill                                  |
| Crawford et al. 2006                               | African penguin <sup>e</sup>  | Anchovy <sup>xiii</sup> , sardine <sup>x</sup>   | Benguela current               | Breeding success  | Positive correlation  |
| Frederiksen et al. 2006                            | Atlantic puffin <sup>m</sup> , black-legged kittiwake <sup>i</sup> , European shag <sup>i</sup> , Chinstrap penguin <sup>ac</sup>                       | Lesser sandeel <sup>ll</sup>   | North Sea (Isle of May)        | Breeding success  | Positive correlations 1973–2003   |
| Croll et al. 2006                                  |   | Antarctic krill <sup>vii</sup>   | Southern Ocean                 | Adult body mass, and breeding success                           | Positive correlations   |
| Jodice et al. 2006                                 | Black-legged kittiwake <sup>i</sup>   | Pacific herring <sup>xiv</sup> , Sandlance <sup>xv</sup> , Capelin <sup>v</sup>          | Gulf of Alaska                 | Female daily energy expenditure                                 | Positive correlations   |
| Louzao et al. 2006                                 | Balearic shearwater <sup>ad</sup>   | Discards and pelagic fish  | Mediterranean Sea              | Breeding success  | Positive correlations 1997–2004   |
| Österblom et al. 2006                              | Common guillemot <sup>d</sup>   | Sprat <sup>xvi</sup>   | Baltic Sea                     | Fledging mass   | Negative correlation 1974–2004  |
| Suryan et al. 2006                                 | Black-legged kittiwake <sup>i</sup>   | Pacific herring <sup>xiv</sup> , Pacific sandlance <sup>xv</sup> , Capelin <sup>vi</sup> | Gulf of Alaska                 | Breeding success  | Positive correlations, but also top-down effects of predation   |
| Becker et al. 2007                                 | Marbled murrelet <sup>ae</sup>  | Krill <sup>xvii</sup> , rockfish <sup>xviii</sup>  | California current             | Breeding success  | Positive correlation 1995–2003  |
| Crawford et al. 2007                               | Cape gannet <sup>f</sup>  | Sardine <sup>x</sup> , anchovy <sup>xiii</sup>   | Benguela current               | Breeding numbers  | Positive correlation 1950s to 2006  |
| MacLeod et al. 2007                                | Harbour porpoise <sup>af</sup>  | Sandeels <sup>xii</sup>  | North Sea                      | Starvation mortality rate                                       | Starvation rate higher in 2002, 2003 when sandeel abundance was low                                     |
| Wanless et al. 2007                                | Black-legged kittiwake <sup>i</sup>   | Lesser sandeel <sup>ll</sup>   | North Sea (Isle of May)        | Breeding success  | Positive correlation 1986–2004  |
| <b>Food quality</b>                                |   |  |                                |   |   |
| Pierotti and Annett 1990, Annett and Pierotti 1999 | Western gull <sup>c</sup>   | Fish (proportion in diet)  | California current             | Breeding success  | Positive correlation  |
| Golet et al. 2000                                  | Pigeon guillemot <sup>ag</sup>  | Pacific sandlance <sup>xv</sup> /Pacific herring <sup>xiv</sup> (proportion in diet)     | Gulf of Alaska                 | Breeding success  | Positive correlation 1989–1997  |

Table 1 (Continued)

| Reference  | Predator   | Prey  | Region  | Life-history parameter            | Analysis   |
|--|--|---|---|-----------------------------------|--|
| Litzow et al. 2002<br>Davoren and Montevecchi 2003 | Pigeon guillemot <sup>ag</sup><br>Common guillemot <sup>d</sup>  | Pacific sandlance <sup>xv</sup><br>Capelin <sup>y</sup>   | Gulf of Alaska<br>Newfoundland-Labrador Shelf | Chick survival<br>Chick condition | T-test two colonies 1995–1999<br>Significant decline when prey energy decrease |
| Wantless et al. 2005                               | Common guillemot <sup>d</sup>                                    | Lesser sandeel <sup>lia</sup> /sprat <sup>xvi</sup><br>calorific content                            | North Sea (Isle of May)                       | Breeding success                  | Significantly lower energy levels likely reason for breeding failure 2004      |
| Österblom et al. 2006<br>Thayer and Sydeman 2007   | Common guillemot <sup>d</sup><br>Rhinoceros auklet <sup>ah</sup> | Sprat <sup>xvi</sup> condition<br>Northern anchovy/Pacific saury <sup>xy</sup> (proportion in diet) | Baltic Sea<br>California current              | Fledging mass<br>Chick growth     | Positive correlation 1997–2004<br>Positive/negative correlation 1993–2003      |
| Wantless et al. 2007                               | Black-legged kittiwake <sup>i</sup>                              | Lesser sandeel <sup>ll</sup> length   | North Sea (Isle of May)                       | Breeding success                  | Positive correlation 1997–2004   |

adult survival rate or population size (Erikstad et al. 1998, Weimerskirch et al. 2001), and this conclusion is supported by experimental manipulations altering food supply to seabirds, although some of these also show that adult survival rates can be affected too (Gill et al. 2002, Davis et al. 2005).

Seabirds, seals and sea lions are central place foragers during the breeding season, tending to occur in large colonies/rookeries on isolated islands free of predators and disturbance. During this period they are constrained to forage within a certain distance of the breeding site, and so are limited to resources located within that defined local area. Central-place foraging may lead to prey depletion or interference competition, especially around large colonies (Furness and Birkhead 1984, Hunt et al. 1986, Birt et al. 1987, Lewis et al. 2001, Forero et al. 2002, Ainley et al. 2003, 2004). These constraints suggest that populations of central-place foragers may be limited by food abundance in the vicinity of colonies, and not by food supplies during the nonbreeding period when top predators can disperse much more widely in relation to food distribution. As predicted, a number of empirical studies show that many seabirds exhibit greatly reduced breeding success when the abundance of their preferred food is depleted (Montevecchi 1993, Phillips et al. 1996, Frederiksen et al. 2005, Furness 2007).

However, recent work has indicated that not only abundance and availability of food, but also food quality can be an important factor in determining population dynamics of some marine top predators (Table 1, Box 1). Indeed, in a few cases, food quality is more important in determining breeding success than is food abundance.

### The junk-food hypothesis – a mechanism for observed dynamics?

A dramatic decline of Stellers sea lions in the Gulf of Alaska since the 1970s has caused widespread concern. One popular explanation for this decline is the ‘junk-food hypothesis’ (Alverson 1992). According to this hypothesis, a shift from high-lipid to low lipid prey in the area (Anderson and Piatt 1999) and presumably in sea lion diet (Sigler et al. 2004, Womble et al. 2005, Trites et al. 2007) has been detrimental to the sea lions, as they are unable to obtain sufficient energy reserves from low-energy prey (Rosen and Trites 2004, 2005). Although laboratory studies clearly have indicated that Stellers sea lions were unable to maintain their weight fed ad libitum low energy prey (Rosen and Trites 2000, Donnelly et al. 2003), and that the seasonal dynamics of the energy content of this prey clearly is out of phase with sea lion reproductive cycles, thus potentially exacerbating the suggested mechanism (Kitts et al. 2004) the relevance of the junk-food hypothesis for the sea lion decline is a subject of much debate. One critical review failed to find clear evidence for the junk-food hypothesis (Fritz and Hickey 2005), but there seems to be substantial evidence that juvenile growth rates and survival were depressed during the population decline, indicating that low energy prey can explain part of the population decline (Trites and Donnelly 2003), while Wolf et al. (2006, p. 289) concluded that the “weight of current

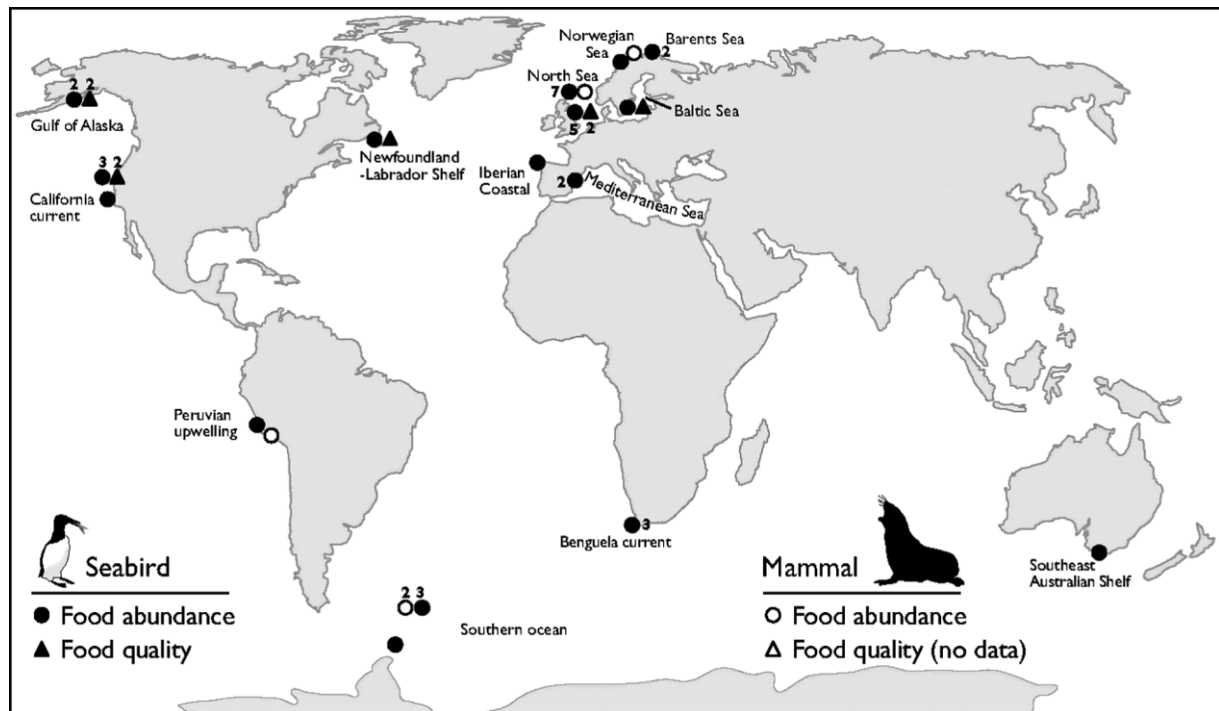


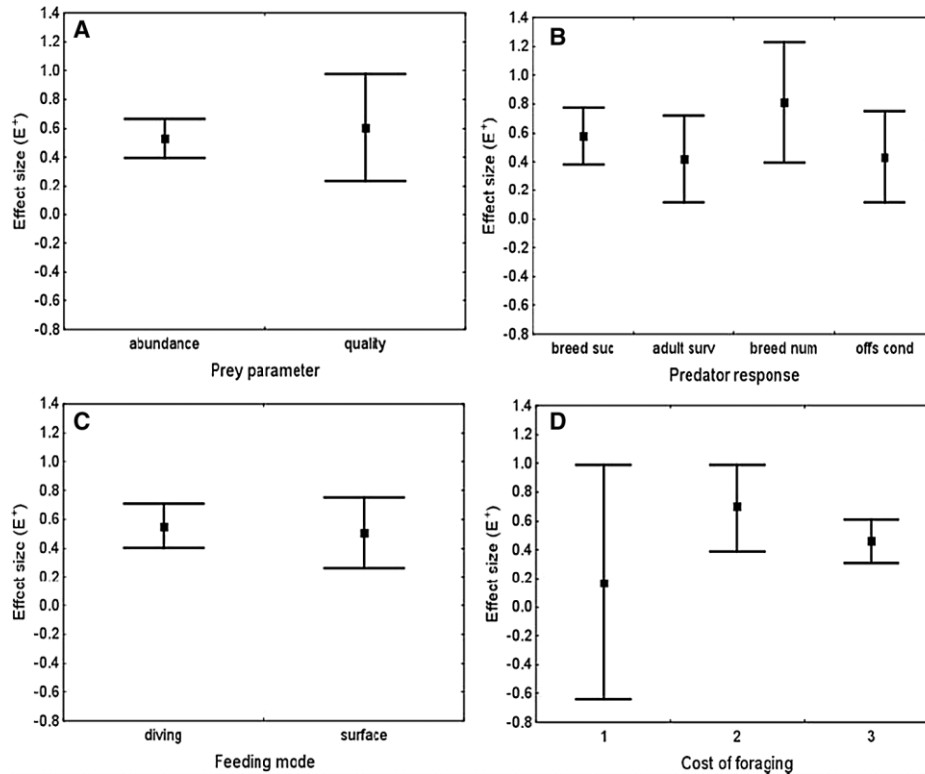
Fig. 1. Map depicting the location of studies and type of interaction listed in Table 1. Numbers refer to the total number of studies (i.e. >1) in each location found in the table.

#### BOX 1. A meta-analysis of predator response to changes in prey abundance and quality

We used Web of Science to locate relevant peer-reviewed articles containing statistical tests of interactions between predator population dynamics or life history parameters and independently assessed dynamics of their prey (abundance or quality). Combinations of the keywords: marine predator/seabird/marine mammal/seal/sea lion/whale/dolphin/porpoise and fish/food/prey abundance/availability/quality were used to locate the articles. A small number of additional studies were located in the reference lists of these publications. We excluded behavioural response (e.g. changes in diet composition or geographic distribution) and focused on responses that can have an impact on the population level. Documented response (or lack of response) was included in the meta-analysis only if real regression analyses were performed between predator and prey parameters. However, in Table 1 we also included studies documenting response to changes in food abundance/quality without such tests (e.g. 'significantly different breeding success between years of documented high and low food abundance'). For the studies that qualified, we performed a meta-analysis of the obtained information. To establish a normalized and variance-stabilized effect size, all correlation coefficients (Pearson's  $r$ ) were converted to a normal distribution ( $rz$ ) using Fischer's  $z$  transform. This allows a weighted analysis to be performed, where the effect size is weighted for the  $i$ th study by the reciprocal of its sampling variance. We first calculated the overall effect size ( $E^{++}$ ) of the predator and prey parameters. We then tested whether the magnitude of the response was influenced by four different characteristics: 1) prey parameter (abundance or quality of prey), 2) predator response (adult condition, adult survival, breeding numbers, breeding success, offspring condition or growth), 3) feeding mode (surface feeders or divers, generalists or specialist) and 4) cost of foraging (using a scale from 1–4, where 1 is low and 4 is high, cf. Furness and Tasker 2000). Since almost all prey species (except in two studies) are high-energy prey, we did not include this factor in the meta-analysis. The total overall effect size ( $E^{+++}$ ) and the corresponding 95% CI were calculated for all target variables as outlined by Rosenberg et al. (2000). An overall effect is considered to be significant if the CI does not include zero (Gurevitch et al. 2000). The group effect size ( $E^+$ ) and the CI were calculated for each of the four above-mentioned characteristics. For each group effect size, the 95% CIs were calculated by bootstrapping 999 randomizations. This nonparametric method creates a distribution of effect sizes based on the actual data set without making any assumptions about the form of the underlying distributions. Non-overlapping CIs indicate significantly different group effect sizes. We tested for differences in effect sizes between characteristics by computing heterogeneity (heterogeneity test), within groups and between groups, an approach analogous to analysis of variance. All calculations were performed using MetaWin 2.0 (Rosenberg et al. 2000).

The results of the analysis show that there was a significant overall effect on predator response from the dynamics (abundance or quality) of their prey. Total effect size ( $E^{+++}$ ) was 0.54 (95% CI = 0.42–0.66). Interestingly, there was no

significant difference ( $p=0.71$ ) between the effects of prey parameter, i.e. abundance and quality (Fig. A). Prey abundance and quality can be inter-related and this finding (based on few studies on quality) could suggest that the two parameters are equally important in affecting predators. Surprisingly, we did not find any significant differences ( $p=0.56$ ) between the observed predator response variables and could thus not indicate which parameter (e.g. offspring condition or adult survival) that was most sensitive to changes in the prey base (Fig. B). There were no significant differences ( $p=0.78$ ) in the effects on feeding mode (diving species or surface feeders, Fig. C), between specialists and generalists ( $p=0.86$ ) or depending on cost of foraging ( $p=0.086$ ) – although this last analysis contained too few species in categories 1 (lowest cost of foraging) and 4 (highest cost of foraging) to draw any conclusions (Fig. D). Predator parameters for the analysis are given in Appendix 1.



evidence is that it is indeed food [causing the population decline] – and both the quantity and quality of the food matters”. Possibly, predation by killer whales *Orcinus orca*, bycatch and direct killing of sea lions have also contributed to this decline (Hennen 2006, Wolf et al. 2006, Trites et al. 2007).

Several seabird species have declined in the same region and the same hypothesis has been suggested as a plausible mechanism (Piatt and Anderson 1996, Anderson and Piatt 1999). Pigeon guillemot *Cephus columba* in the Gulf of Alaska declined substantially during several decades, and chick survival was substantially higher in areas where chicks were fed a high energy diet than when fed a diet of low energy content (Litzow et al. 2002). Pigeon guillemots also provide support for the hypothesis that predators trade off prey quality (lipid content) for consistent abundance of prey (Litzow et al. 2004), indicating that they will select high energy content foods when they can avoid risk of experiencing low prey availability (Skov et al. 2000).

Western gulls *Larus occidentalis* had a higher breeding success when feeding on an energy rich diet (Pierotti and Annett 1990, Annett and Pierotti 1999). Paiva et al. (2006) also reported that little terns *Sterna albifrons* achieved better chick growth rates when they were able to select high-energy food fish.

Decreased abundance and reduced energy content of seabird prey in the North Sea led to a massive breeding failure of seabirds in 2004. Although there is clear evidence that reduced abundance of sandeels leads to reduced breeding success of sensitive seabird species (Furness and Tasker 2000), such as Arctic skuas *Stercorarius skua* and kittiwakes (Phillips et al. 1996, Furness 2007), the common guillemot *Uria aalge* continued to breed with essentially normal success rates through the period of low sandeel abundance at Shetland (Mavor et al. 2006). However, the common guillemot showed greatly reduced breeding success in much of the northwest North Sea in 2004. In this case, although food abundance was low, the rate of provisioning

of common guillemot chicks was normal but chick growth was poor due to the low energy content of the food fish, suggesting that the breeding failure of this species was due to the energy content of the fish rather than low food abundance (Wanless et al. 2005). In addition to these empirical field observations of seabirds, a recent paper (Kitaysky et al. 2006) illustrated a plausible mechanistic explanation for reduced seabird chick survival (potentially explaining part of the population decline in the Gulf of Alaska) when fed a diet of low energy. Chicks of red-legged kittiwakes *Rissa brevirostris* that were experimentally fed fish of low energy content had an impaired cognitive ability likely resulting in reduced capabilities to obtain food for themselves once they fledged (Kitaysky et al. 2006). This experimental study of seabirds, together with the captive feeding experiment of sea lions (Rosen and Trites 2000, 2004) and seabirds (Dahdul and Horn 2003), and supplementary feeding experiments giving higher quality food to wild seabird chicks (Romano et al. 2006) provide some of the strongest evidence for the junk-food hypothesis in marine ecosystems.

Although not intended as an experiment, food web dynamics in the Baltic Sea have also provided a neat test of the junk-food hypothesis. Common guillemot fledgling body mass was significantly positively correlated to body condition (a proxy for energy content) of their prey (sprat *Sprattus sprattus*) during a period of 30 years (Österblom et al. 2006). In this example, sprat condition showed a negative correlation with sprat stock size, indicating that sprats were competing for food and was unable to achieve high body condition when their population size was high. Thus, counter-intuitively, common guillemot chick growth was best when sprats were scarce rather than abundant in the ecosystem. These trends were consistent over a period of stable conditions, rapidly deteriorated energy content and a period of increasing energy content, thus providing a unique example of junk-food effects from the field. The limited number of field studies summarized in Table 1 and analyzed in Box 1 illustrates the impact of food quality on some marine predator life-history parameters. Food quality is however not only important in the context of marine top predators described here, but can be seen as an important influence on food web structure in a wide variety of ecosystems. For example, nutritional quality of plants affects the predator-prey interactions between ladybirds (Giles et al. 2002).

## Drivers of 'junkiness'

The junk-food hypothesis has support in empirical and experimental data, but what factors influence the emergence of junk-food? The dynamics differ between the examples described above and alternative/complementary mechanisms have been proposed for these systems. In the Gulf of Alaska, several hypotheses have been suggested, e.g. a climate-related regime shift. According to this hypothesis, a rapid change in atmospheric/oceanographic conditions in the mid 1970s caused a substantial restructuring of the ecosystem, resulting in a large-scale change in species composition, i.e. from a predominantly forage fish (species of high energy content) – to a predominantly pollock

*Theragra chalcogramma* (low energy content) dominated ecosystem. There appears to be substantial evidence indicating that climatic conditions were the main driver of these changes (Trites et al. 2007), although potential top-down effects (i.e. fishing) or food web related mechanisms (predation/competition) appear to have been less studied.

In the North Sea, one hypothesis is that climate-related changes in geographical distribution of zooplankton (mediated by changes in ocean temperature: Beaugrand et al. 2002) created deteriorating feeding conditions for lesser sandeel *Ammodytes marinus*, which negatively affected their reproduction and feeding conditions, thus leading to a decreasing stock of fish in poor body condition (Wanless et al. 2005). Also this climatological change has been referred to as a regime shift (Beaugrand 2004). However, the dynamics of herring *Clupea harengus* indicate that other hypotheses also are plausible (Frederiksen et al. 2007). There is a strong negative correlation between herring and sandeel stock sizes (Frederiksen et al. 2007) potentially suggesting top-down control (Worm and Myers 2003).

In the Baltic Sea, the reduced condition of common guillemot chicks is not a result of changes in prey species composition (as in the Gulf of Alaska) or of decreasing stocks (and condition) of preferred prey (as in the North Sea). Instead, a deteriorated condition (lower fat content) of the preferred prey during a period of rapid increase of that prey population, i.e. sprat *Sprattus sprattus* – a density dependent mechanism, where intra- and interspecific (i.e. herring) is the most plausible explanation for the dynamics (Casini et al. 2006). A climate-related regime shift has been suggested to be responsible also for these dynamics (Alheit et al. 2005), and although above average temperatures during the 1990s favoured sprat reproduction (MacKenzie and Köster 2004), the most likely mechanism for the dramatic population increase is reduced predation from cod (the main predator of sprat: Österblom et al. 2006). The cod stock in the Baltic Sea was substantially reduced as a result of a combination of high fishing mortality and poor reproductive conditions. Although cod predation previously was the main cause of mortality of adult sprat, currently, fishing is the main driver of adult sprat stock numbers.

## Junk-food and population viability

The meta-analysis performed in this review (Box 1) indicate there is a strong effect of both prey abundance and prey quality on predator parameters. This result is likely to be biased by a larger likelihood of publishing significant interactions (Gurevitch and Hedges 1999) and we urge colleagues to also publish other results (e.g. the approach used by Reid et al. 2005). Why should some species be sensitive to the energy levels in their prey while others are sensitive to prey abundance/density? What is the minimum prey abundance required for good predator performance, and/or at what minimum prey quality would a population do well? The answers to these questions will differ between species and their sensitivity to changes in prey abundance and/or quality. This sensitivity will be affected by prey handling capacity (single- or multiple prey loaders), cost of foraging and digestive efficiency. It seems that common

guillemots may be particularly vulnerable to reductions in prey quality because they are single-prey loaders. They carry only one fish at a time from the sea back to their chick on the cliffs. Much of the time, and energy, spent in foraging by common guillemots is spent in travel between the foraging area and the colony, which is particularly expensive for a bird with an exceptionally high wing loading and low load carrying capacity. Carrying a single fish of low energy content simply does not pay in this situation. In contrast, most seabirds carry several fish at a time, and so the importance of energy content of each fish is less pronounced, and the benefit of being able to catch many fish in a short time (high prey density) is more evident. In addition to these considerations, seabird species may differ considerably in their digestive strategy. Digestive efficiency in seabirds decreases with decreasing lipid/energy content of their prey (Brekke and Gabrielsen 1994) and the digestive efficiency of seabirds differs greatly between species, in part as a result of anatomical adaptations that trade off digestive efficiency for reduced mass of the alimentary tract to promote greater foraging efficiency in highly active species (Hilton et al. 2000a). Common guillemots are at one extreme, with a relatively low digestive efficiency but a relatively reduced alimentary tract mass (Hilton et al. 2000a).

The resilience of seabird populations to changes in prey abundance and availability has focused the attention on adaptive capacity of species related to foraging strategies (Furness 2003), but the 'junk-food' observations reviewed in this study indicate that the flexibility of seabird digestive systems (Hilton et al. 1998, 2000b) can be equally important for understanding the resilience of seabird populations to changes in feeding conditions.

Trites et al. (2007) have suggested that an outbreak of epidemic disease in sea lions could have been related to increased oxidative stress due to the poor diet and thus increased susceptibility to disease. Interestingly, avian cholera was detected for the first time in common guillemots in the Baltic Sea in 1998 (Österblom et al. 2004), simultaneously to record low condition of sprat (Österblom et al. 2006). In addition, adult survival of guillemots in the area was significantly lower during the 1990s (junk-food period) when compared to prior to this period (high energy food: Olsson et al. 2000).

## Junk-food and ecosystem resilience

Biological diversity appears to play a substantial role in ecosystem resilience and in sustaining desirable ecosystem states (Elmqvist et al. 2003). Response diversity, defined as 'the variability in response of species within functional groups to environmental change' (Elmqvist et al. 2003) has been illustrated in this review by the sensitivity of marine mammals and seabirds to prey quality. This quality-aspect of predator response to changes in their prey base adds a level of complexity in the challenge of managing marine ecosystems sustainably, especially since the loss of response diversity, leading to a loss of resilience, can lead to undesirable regime shifts (Bellwood et al. 2004). Relatively little is known about thresholds at which ecosystems change dramatically, as well as critical levels of food abundance/

quality needed to sustain marine predators. Marine research has focused much attention on the effects of bottom-up (e.g. climate related) forcing, and although this is a highly relevant factor e.g. for seasonal match/mismatch between trophic levels and reproductive success for many fish species, a large number of studies has recently documented the importance of top-down forcing (e.g. fishing and predation) and/or competition (Worm and Myers 2003, Hjermmann et al. 2004, Frank et al. 2005, Halpern et al. 2006). The intellectual and scientific challenge lies in explaining the interactive effects of these factors in order to provide management with adequate decision support.

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#### Appendix 1. Predator parameters used in the analysis

| Predator species        | Mode    | Selection  | Foraging cost |
|-------------------------|---------|------------|---------------|
| African penguin         | diving  | specialist | 3             |
| Antarctic fur seal      | diving  | specialist | 3             |
| Atlantic puffin         | diving  | specialist | 3             |
| Black-browed albatross  | surface | generalist | 1             |
| Black-legged kittiwake  | surface | specialist | 2             |
| Brown pelican           | surface | generalist | 2             |
| Brünnich guillemot      | diving  | specialist | 3             |
| Cape cormorant          | diving  | specialist | 2             |
| Cape gannet             | diving  | generalist | 2             |
| Cassin’s auklet         | diving  | specialist | 3             |
| Common guillemot        | diving  | specialist | 3             |
| European shag           | diving  | specialist | 3             |
| Gentoo penguin          | diving  | generalist | 3             |
| Great skua              | surface | generalist | 3             |
| Macaroni penguin        | surface | generalist | 3             |
| Marbled murrelet        | diving  | specialist | 3             |
| Razorbill               | diving  | specialist | 3             |
| Rhinoceros auklet       | diving  | specialist | 3             |
| South American sea lion | diving  | specialist | 3             |
| Swift tern              | diving  | specialist | 4             |
| Western gull            | surface | generalist | 3             |