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Trophic relationships among capelin (*Mallotus villosus*) and seabirds in a changing ecosystem

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Trophic interactions among seabirds and capelin (*Mallotus villosus*), a key forage species off Newfoundland and Labrador, are examined. During the 1990s, estimates of relative year-class strength of capelin were similar to estimates in the 1980s, capelin spawned later and matured younger, mean fish size was smaller, and there were large-scale distributional shifts of capelin. Most of these changes were linked to below-normal sea temperatures during the early 1990s, but the changes have persisted even though temperatures have returned to normal. Seabirds bred later in the 1990s and changed diets and foraging strategies. Off eastern Newfoundland, the breeding success of black-legged kittiwakes declined during the early 1990s owing to a suite of factors, including their inability to dive to capture capelin, the late arrival of capelin inshore and predation by gulls. Common murres and puffins did not suffer breeding failures because they could dive and catch capelin at depth. Off Labrador, black-legged kittiwakes experienced breeding failures because of the lack of capelin while common murres were able to find alternate prey and bred successfully. The diets of gannets in the 1990s contained a higher proportion of cold-water prey than in earlier periods when warm-water prey predominated. The population sizes of all seabird species remained stable or increased, with the exception of gulls. Increasing populations of seabirds are related in part to their lessened mortality from gillnets since the closures of the eastern Canadian groundfishery in 1992, whereas declining populations of gulls can be related to reduced food availability from fishery discards and offal. This food limitation has led gulls to switch much of their foraging effort from scavenging to predation on seabird adults and chicks before capelin arrive inshore.

Keywords: capelin, gannets, gulls, kittiwakes, Labrador, Leach's storm-petrel, murres, Newfoundland, puffins, seabirds.

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Introduction

Recent trends of fishing species at lower trophic levels (Pauly *et al.*, 1998) have raised concerns that depleted predatory finfish might recover more slowly and that non-commercial predators, such as seabirds, might suffer deleterious effects. The impacts of fishing on seabirds can be direct and indirect, ranging from beneficial to detrimental (Montevecchi, 2001). Therefore, it is critical to understand trophic relationships to elucidate the effect of changing demographic parameters of forage species on higher vertebrates.

The population dynamics of forage fish can be influenced by both the environment and fishing, but the relative effects of these factors are often difficult to identify. Similarly, when seabird biology changes it is difficult to pinpoint the cause, because changes in both prey and physical environment can influence seabird ecology. Consequently, it can be particularly informative if changes in seabird biology can be documented

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when a forage species shows changes in its biology in the absence of a major fishery. This situation may be unusual because there are probably few instances where major prey species of seabirds have not been heavily exploited and, if not exploited, it is likely that little is known of the population dynamics of the prey. In the Newfoundland–Labrador area, capelin (*Mallotus villosus*) is both a major forage and commercial species and, as a result, has been the focus of directed research for about 30 years. Exploitation has not been high, and there is no evidence that the fishery has had a negative effect on the species (Carscadden *et al.*, 2001).

The Newfoundland–Labrador region is an important area for seabirds. Black-legged kittiwakes (*Rissa tridactyla*) and Atlantic puffins (*Fratercula artica*) are abundant. The world's largest colonies of Leach's storm-petrels (*Oceanodroma leucorhoa*) and common murres (*Uria aalge*) are in eastern Newfoundland, as are three of North America's six northern gannet (*Morus bassanus*) colonies (Montevecchi and Tuck, 1987). With the exception of the planktivorous storm-petrels, all these species are highly dependent on capelin, particularly during the breeding season when capelin move from offshore to spawn on Newfoundland and Labrador beaches.

The objective of this paper is to examine the demographic parameters of seabirds and their principal prey capelin, at a time when capelin behaviour and ecology has changed, in an attempt to understand better the trophic interactions in the Northwest Atlantic. We review many aspects of the biology of capelin on the Newfoundland–Labrador shelf, including abundance, distribution, spawning times, and mean sizes, and particularly emphasize changes that occurred during the 1990s. These changes are considered in the context of ocean climate change. We also review the biology of the main seabird species that consume capelin extensively during the breeding season, again with emphasis on the 1990s, when capelin biology changed. Other species with different diets, such as storm-petrels and gulls, are discussed to a lesser extent, and both indirect and direct effects of capelin availability on seabird breeding success are considered.

The marine environment

The south-flowing, cold Labrador Current dominates the oceanography off Newfoundland and Labrador. Long-term changes in the ocean climate are reflected in depth-integrated (0–175 m) water temperatures recorded at Station 27 (Figure 1), east of St John's, Newfoundland (47°31′50″N 52°35′10″W), which has been monitored since 1946. Variations in temperature at this oceanographic station are indicative of changes from southern Labrador to the northern Grand Banks (Drinkwater *et al.*, 1999). Long-term thermal trends

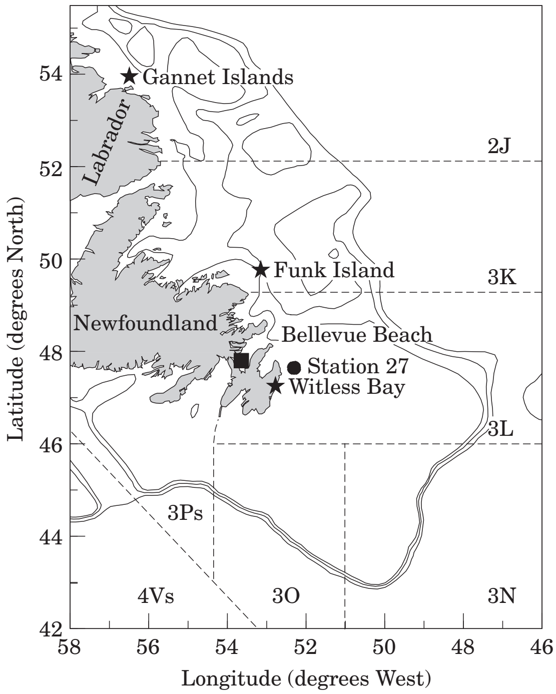

Figure 1. Locations of seabird colonies (stars), hydrographic Station 27 (circle), capelin spawning beach (square) and NAFO Divisions (e.g. 2J, 3K).

reveal a warm period throughout the 1950s and 1960s, a cool period in the early and mid-1970s, a brief warm period during the late 1970s, and an extended cool period from the early 1980s to the mid-1990s. During the mid-1990s, water temperatures returned to average. Annual averages, however, show that 1991 was the coldest year on record and that 1996 was one of the warmest (Colbourne, 2001).

Capelin

Abundance

For several years, assessment of the Northwest Atlantic Fisheries Organization (NAFO) SA2+Div. 3KL capelin stock has centred on the use of a mathematical model to estimate relative year-class strength. Although the 95% confidence intervals are wide and there is uncertainty about the data sources themselves, the overall trends determined through the assessment process indicate that stock status has not changed dramatically over two decades (Anon., 2000). Since the early 1990s, there have been discrepancies between the model output and other sources of information. Offshore acoustic surveys have indicated almost negligible quantities of capelin compared with the 1980s (Carscadden and Nakashima, 1997). Acoustic data, however, have recently been included in the mathematical model, thereby reducing

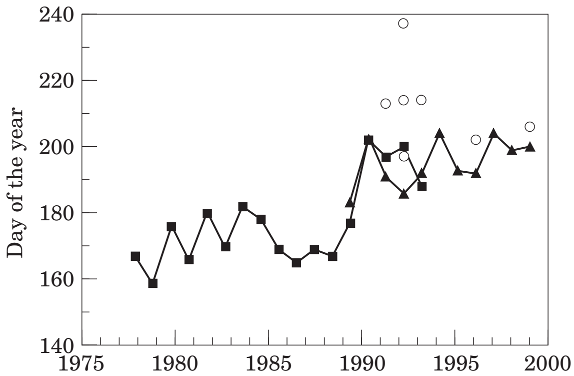

Figure 2. Spawning times of capelin, 1978–2000. Rectangular symbols denote spawning times, after Carscadden *et al.* (1997), triangles denote the earliest spawning observed at Bellevue Beach in a given year, and ovals are later spawnings.

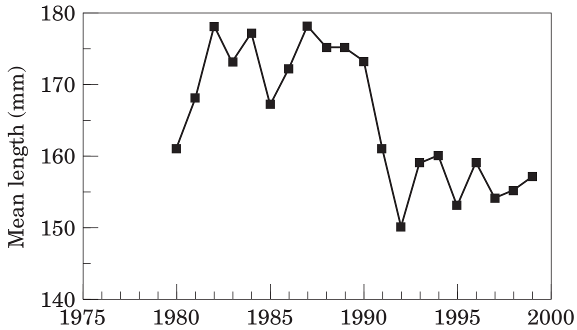

Figure 3. Mean lengths (total length) of mature capelin, 1980–1999.

some concerns about the divergence among indices. Other discrepancies among information for capelin include opinions of inshore fishers and predator diets. Inshore trapnet fishers consider that the capelin stocks were not as abundant in the 1990s as they had been earlier (Carscadden *et al.*, 2001). In addition, capelin has decreased in the diets of some top predators (e.g. murres, Rowe *et al.*, 2000) compared with historical accounts.

Spawning time and mean length

The spawning of capelin on Newfoundland beaches during June and July was a well-known and highly predictable event. During the early 1990s, spawning was later, and this delayed spawning was coincident with smaller average fish length and with cold surface water temperatures. This smaller average fish size was due to smaller mean lengths of fish aged three and older, as well as an increased proportion of spawning two-year-olds (Carscadden and Nakashima, 1997). Carscadden *et al.* (1997) reported that 80% of the variation in spawning time between 1978 and 1994 was significantly and negatively related to mean fish size and sea temperatures that capelin experienced during gonadal maturation. In cold years, maturation and inshore migration was delayed. The linkage between mean fish size and spawning time was not clear, but it may be related to differences in energy storage and different energy expenditures by capelin of different size during their extensive spawning migrations. Since 1990, spawning times have been observed at Bellevue Beach in Trinity Bay (Figure 1). For the five years of overlap (1990–1994) between the previous study (Carscadden *et al.*, 1997) and the Bellevue Beach observations, the earliest spawning times in each year are approximately the same and exhibit similar patterns (Figure 2). From these data, we conclude that capelin spawning has continued to be late through 2000. This continued delayed spawning might seem surprising, given the return of sea temperatures to average conditions during the late 1990s. However, a significant portion of spawning-time variation in the earlier study was explained by mean fish length, and the mean lengths of capelin have continued to be small throughout this period (Figure 3).

Distribution

During the early 1990s, capelin exhibited large-scale changes in distribution within and outside their normal range that have been linked to colder ocean temperatures. Within the normal distribution area in SA2+Div. 3KL, capelin essentially disappeared from Div. 2J adjacent to the Labrador coast, to occupy an area to the south on the northern Grand Banks (Carscadden *et al.*, 2001). By-catch in autumn bottom-trawl surveys and young fish surveys indicated that during 1998, capelin had moved in more northerly and westerly directions that were reminiscent of their traditional seasonal distribution (Anon., 2000). However, this return to a typical autumn distribution did not continue in 1999 and 2000.

Outside their normal distribution area, capelin occurred on the Flemish Cap and eastern Scotian Shelf (Frank *et al.*, 1996). They appeared in those areas during the 1990s and occasionally earlier in the time-series only during cold periods. They were not found there during every cold period, suggesting that cold sea temperatures were a necessary but not a sufficient condition for capelin to occur outside their normal range. Frank *et al.* (1996) documented these unusual appearances on the Flemish Cap until 1994 and on the eastern Scotian Shelf until 1995. Capelin continued to appear on the Flemish Cap in small numbers from 1996 to 2000 in research bottom trawls, in Russian research bottom trawls, and as by-catch in the shrimp fishery (Carscadden *et al.*, 2001; Fisheries and Oceans Canada, unpublished data). On the eastern Scotian Shelf, capelin catches in research bottom trawls remained high until spring 2000; the summer 2000 survey showed a dramatic decline (Carscadden *et al.*, 2001). There, sea temperatures were beginning to warm during the late 1990s, but they were still below the long-term mean (Drinkwater *et al*., 1999).

Seabirds

Diets

The diets of gannets have been studied for 25 years in a large colony on Funk Island off the northeast coast of Newfoundland (e.g. Montevecchi and Myers, 1996). Gannet diets exhibited a shift from predominantly migratory warm-water species during the late 1970s through the late 1980s, to predominantly cold-water species during the 1990s. The warm-water species suite was characterized by mackerel (*Scomber scombrus*) in most years while the cold-water suite included high proportions of capelin. The pronounced increase of capelin in the diet in the early 1990s coincided with a delayed inshore migration of that species, so making them available to gannets during the chick-rearing period. The absence of mackerel, on the other hand, was probably due to their restricted migration into this northern area because of the colder water. The switch to a diet of primarily capelin during the 1990s did not appear to affect the breeding success of gannets (Montevecchi and Myers, 1996).

The sharp decline in capelin abundance off Labrador in the early 1990s was reflected in the diets of common and thick-billed murres. During the 1990s, both species ate less capelin and more daubed shannies (*Lumpenus maculatus*) than in the 1980s (Bryant *et al*., 1999). Common murres had formerly been observed feeding heavily on capelin and, as a result, capelin were considered critical for murre success. On the other hand, thick-billed murres had a more varied diet and were considered more adaptable. Bryant *et al*. (1999) found that, in 1996 and 1997, the diets of murres and their time at sea changed but that feeding rates, chick growth, breeding success, and adult mass did not. Daubed shannies are as energy-rich as capelin and this may have contributed to the unchanged breeding success. Atlantic puffins breeding in southern Labrador and in eastern Newfoundland have also bred successfully in the absence of mature capelin (Russell, 1998; Baillie, 2001).

A recent study of the winter diet of murres in coastal Newfoundland revealed that, although the proportion of fish in the diet did not change between the 1980s and 1990s, both Arctic cod (*Boreogadus saida*) and capelin declined in frequency of occurrence during the 1990s. The zooplankton portion of the diet also shifted from predominantly euphausiid to predominantly amphipod (Rowe *et al*., 2000). The authors expressed concern over the increased reliance of murres on crustaceans as opposed to the predominantly capelin diet during the 1950s (Rowe *et al*., 2000). It is striking that capelin are declining in some seabird diets and that the capelin taken by murres have decreased in size and condition throughout the 1990s (G. K. Davoren and W. A. Montevecchi, unpublished data).

Time budgets

Although breeding success of common murres was not affected by the sharp decline in capelin abundance off Labrador in the 1990s, they changed their feeding strategy, diving deeper and capturing solitary prey, instead of capturing pelagic, schooling capelin. In addition, breeding pairs spent less time together at nest sites and increased foraging effort at sea (Bryant *et al*., 1999). This flexible parental foraging behaviour has also been reported for murres breeding at Witless Bay (Burger and Piatt, 1990) and elsewhere (Uttley *et al*., 1994). Capelin availability decreased by an order of magnitude at Witless Bay over two successive breeding seasons in the mid-1980s. Common murre breeding success was unchanged because parents spent more time foraging (Burger and Piatt, 1990), making breeding success less sensitive to fluctuations in prey availability.

Timing of breeding

Like capelin spawning, seabird breeding has been later during the 1990s; however, direct comparisons are difficult because of a lack of comparable data prior to the 1990s. At Witless Bay, mean laying dates for black-legged kittiwakes were about 7–10 days later during 1992 and 1993 than in 1969 and 1970 (Maunder and Threlfall, 1972; Regehr and Montevecchi, 1997). At the Gannet Islands off southern Labrador, egg-laying by kittiwakes and murres was later during the period 1996–1998 than in the early 1980s (Hipfner *et al*., 2000). At Funk Island, murres also started breeding 2–3 weeks later in the early 1990s (G. K. Davoren and W. A. Montevecchi, unpublished data). At Witless Bay, murres, puffins, herring gulls (*Larus argentatus*) and great black-backed gulls (*L. marinus*) exhibited delayed breeding in 1992 and 1993. Capelin arrival was reportedly delayed more than seabird breeding, resulting in reduced survival of the early-hatching chicks of some species (Regehr and Montevecchi, 1997).

Breeding success

Breeding success has been studied extensively for black-legged kittiwakes, because cliff nests are easily surveyed at colonies and breeding performance is variable owing to a range in clutch size from one to three eggs. Kittiwakes are surface-feeding piscivores and, therefore, are highly sensitive to changes in the vertical distribution of prey in the water column. The relationship between breeding success and prey availability has been complicated by indirect fishery and trophic effects.

The breeding success of kittiwakes in Witless Bay was higher in 1969 and 1970 than in the period 1990–1993 (Regehr and Montevecchi, 1997). Chardine (1996) showed somewhat higher success in 1994 and 1995, but overall reported that breeding failures were severe between 1990 and 1995. Breeding-success data have not been reported since then, although Hipfner *et al*. (2000) and Jamieson (2000) both reported that kittiwake breeding success improved after 1996.

The successive breeding failures of kittiwakes in eastern Newfoundland are attributable to prey availability, predation, and their interactions. At Witless Bay, kittiwakes and large gulls (herring and great black-backed gulls) feed capelin to their chicks. Owing to the elimination of groundfishery discards and offal, gulls have undergone population declines (Montevecchi, 2001). This food-stress caused by the lessened availability of offal, combined with the late inshore arrival of capelin in the early 1990s, resulted in heavy predation by gulls on kittiwake chicks (Regehr and Montevecchi, 1997). Once capelin arrived inshore, predation by gulls on kittiwake chicks declined substantially. Gull predation attempts on kittiwake chicks were more frequent after gull chicks hatched and before capelin arrived, compared with the period before gull chicks hatched and after the arrival of capelin inshore (Massaro *et al*., 2000). Similar interactions were observed between gulls, capelin, and Leach's storm-petrels during 1996 and 1997 (Stenhouse and Montevecchi, 1999), and during the 1970s (Pierotti and Annett, 1991).

Although the breeding success of kittiwakes was poor during the early 1990s in Witless Bay, the breeding success of pursuit-diving seabirds, such as murres and puffins, did not decline. This suggests that capelin were available in sufficient quantities for seabirds that dived for food.

At the Gannet Islands, kittiwakes experienced low breeding success during the 1990s (Hipfner *et al*., 2000), and in 1984 and 1985 (Birkhead and Nettleship, 1988). In 1984 and 1985, spring ice from the Arctic was heavy and sea surface temperatures were cold off Newfoundland and Labrador, including in Witless Bay, where kittiwakes also experienced failures. Severe oceanographic conditions were not considered to be an important factor in the poor breeding success between 1996 and 1998 because ocean conditions had begun to ameliorate after the harsh conditions of the early 1990s. In fact, breeding success improved at Witless Bay in 1996, in contrast to the poor breeding in Labrador. The difference in breeding success between the two sites was attributed to the presence of capelin in the more southern region and the absence of capelin in the north (Hipfner *et al*., 2000).

Population trends

The Canadian Wildlife Service website provides a general overview of the status of seabirds in Canada and represents a consensus among seabird biologists familiar with the seabirds in each region.

Common murres, razorbills, and Atlantic puffins appear to be increasing off Newfoundland and Labrador, although population censuses have been sporadic. The breeding population of common murres at Funk Island has been stable at 340 000–400 000 pairs during the period 1980–2000. The population of common murres at Witless Bay is increasing and consists of approximately 100 000 breeding pairs (Canadian Wildlife Service, unpublished data). Similarly, the most recent population estimate for Atlantic puffins at Great Island in Witless Bay was 123 000 pairs, an increase from an earlier estimate in 1979 (Rodway *et al*., 1996). Recent increases in the populations of auks may be attributed to the reduced number of gillnets in Newfoundland waters following the closure of the eastern Canadian groundfishery in 1992 (Montevecchi, 2001) and to a reduction in illegal hunting and egg collection during the 1980s and early 1990s (Montevecchi and Tuck, 1987; Montevecchi, 2001; J. W. Chardine, unpublished data).

Breeding populations of northern gannets have also increased from the mid-19th century (Montevecchi and Myers, 1997) and in recent decades (Chardine, 2000). The long-term increases were related to a combination of reduced exploitation, immigration, and warmer sea temperatures that favoured the migration of mackerel into the region during the breeding season (Montevecchi and Myers, 1997). More recent increases may be related to decreased pressure from by-catch mortality. Extensive breeding failures experienced by black-legged kittiwakes in Newfoundland during the early 1990s (Regehr and Montevecchi, 1997) did not appear to affect the number of long-lived breeding adults (J. W. Chardine, A. W. Diamond, R. D. Elliott, and A. R. Lock, unpublished data). The status of Leach's storm-petrel is unknown.

Discussion

This review of recent studies on capelin and seabirds and ocean changes in the Northwest Atlantic not only confirms the linkages between the species but also illustrates the complex relationships among them and the physical environment. For capelin, the incidence of late spawning and large-scale distributional changes were associated with below-normal sea temperatures. Sea temperatures have returned to normal whereas late spawning times and unusual distribution patterns persist. Smaller fish sizes combined with lower age at maturity have also persisted throughout the 1990s. While the overall trends determined through the assessment process indicate that the stock status has not changed dramatically over two decades, discrepancies among indices and between indices and the assessments results need to be resolved.

Some of the changes in seabird ecology during the 1990s echo changes in capelin biology. Capelin spawned later than normal throughout the 1990s and most seabird species exhibited delayed breeding. Temperature, operating directly or indirectly, possibly through the timing of spring zooplankton production, appears to affect the timing of maturation and spawning of capelin. It is not clear, however, what mechanisms mediate the late breeding of seabirds. Seabirds return to colonies and lay their eggs before capelin move inshore, so the onset of copulation and egg formation is obviously not influenced by something as simple as the delayed inshore migration of capelin. Little is known of the activities and diets of seabirds in the few months before and during egg-laying. Studies examining diets would allow assessments of the determinants of the onset of laying. Birds such as kittiwakes that regurgitate their food, and planktivores such as storm-petrels, would be tractable and informative study species for such research. Stable isotope analyses of tissue would identify the trophic positions of different avian species during egg development.

Factors influencing seabird breeding success are clearly multifaceted and variable among species (Montevecchi, 1993). Given trends in capelin year-class strength and the fact that populations of most seabirds that feed on capelin are stable or increasing, the availability of capelin does not appear to be low. It is essential, however, to differentiate abundance from availability, which has a clear influence on surface-feeding piscivores such as kittiwakes. Periods of poor availability of capelin (i.e. depth distribution in relation to diving abilities; timing of arrival inshore in relation to avian breeding) have occurred both among and within years. The late arrival of capelin affected kittiwakes and storm-petrels through food shortage and increased gull predation. Predation by gulls on kittiwakes during the 1990s may have been the most intense that kittiwakes ever experienced and had a marked detrimental effect on their breeding success.

These results provide insights into the thesis of using seabirds as biological indicators. The high breeding success of pursuit-divers relative to surface-feeders during the 1990s indicates that monitoring the entire suite of seabird species is essential to obtaining adequate information about the status of capelin. The successful breeding by murres at the Gannet Islands off Labrador using an alternate foraging strategy also illustrates that breeding success alone can be a poor indicator of prey availability. Although common murres and puffins were believed to depend on capelin for successful breeding, this proved to be untrue. A combination of shorter-term aspects of avian ecology such as time-energy budgets, offspring conditions or diets may provide more informative and robust indicators of prey conditions (Cairns, 1987).

With our current state of knowledge, it is possible that the most valuable and reliable information comes when large-scale changes occur. For example, at the Gannet Islands, the lack of capelin in the diet of all seabirds mirrored information from other sources about the decline of capelin off the Labrador coast. In the Northeast Atlantic, adult mortality of murres increased markedly in the late 1980s, consistent with the decline of the Barents Sea capelin (Vader *et al.*, 1990). In the Northwest Atlantic, the shifts in gannet diets provided some of the first indications of major shifts in pelagic foodwebs on the Newfoundland–Labrador Shelf. The switch to cold-water fish confirmed, and was consistent with, other observations of ocean cooling and the late arrival of capelin inshore. This also added insights on how animals adapt to large changes in the physical and biological environment. Comparisons of breeding success of surface-feeding kittiwakes and pursuit-diving auks at Witless Bay and the Gannet Islands led to the conclusion that capelin were probably approaching the beaches at greater depths during the early 1990s than during periods when kittiwakes bred successfully. There was no at-sea capelin research during those seasons, and this information on capelin depth distribution during a period of below-normal sea temperatures was novel.

This review has highlighted the complex interactions among several seabird species, their principal prey, and human activities in the Newfoundland and Labrador region. Generally, the capelin data came from single-species long-term studies. In contrast, many of the seabird data were derived from directed studies on seabirds and their prey. However, with the exception of the gannet feeding observations, the seabird studies spanned only a few breeding seasons. There is an obvious need for long-term monitoring of the interactions between seabirds and their prey, both within and outside breeding seasons. Seabirds have long lifespans and the influences of variations in prey availability on seabird population dynamics may be subtle and long term.

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