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Centurial and decadal oceanographic influences on changes in northern gannet populations and diets in the north-west Atlantic: implications for climate change

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Millennial and centurial changes in oceanography influence the distributions and movement patterns of fish and invertebrates. These changes, in turn, determine the availability of food resources for higher trophic levels and, hence, affect the distributions and abundances of marine birds. A century-long population trend of northern gannets (*Sula bassana*) is correlated with warming surface water conditions and increased mackerel (*Scomber scombrus*) availability. On a decadal scale, a major dietary change of breeding gannets from migratory warm-water pelagic fish and squids to cold-water fish is associated with cold-water perturbations in the north-west Atlantic during the 1990s. Cold-water influences appear to have inhibited migratory pelagic fish and squid from moving into the region in recent years, causing a major shift in pelagic food webs on the Newfoundland Shelf. Such findings imply that slight changes in oceanographic conditions, possibly associated with climate warming, could have large-scale and pervasive effects on seabird distributions, feeding ecology, reproductive success, and populations. Such changes might be detected initially near the limits of seabird ranges and the margins of oceanographic regions.

Key words: climate change, feeding ecology, gannets, north-west Atlantic, oceanography, seabird populations, trophic interactions.

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Introduction

Oceanographic influence on marine predator–prey relationships is evident in millennial and centurial changes in seabird distributions and populations (Montevecchi and Hufthammer, 1990; Montevecchi and Kirk, 1996). Decadal variation in ocean conditions is associated with changing reproductive and dietary aspects of seabird ecology (Ainley *et al.*, 1986; Bertram and Kaiser, 1993; Chastel *et al.*, 1993; Montevecchi and Myers, 1996). Both centurial and decadal anomalies in ocean temperature have been documented in the north-west Atlantic (Montevecchi and Myers, 1992; Colbourne *et al.*, 1994; Drinkwater *et al.*, 1994). Sea-surface temperature anomalies have influenced the movements of migratory warm-water fish (Montevecchi and Myers, 1996) and have markedly delayed the inshore migration of beach-spawning capelin (*Mallotus villosus*; Nakashima, 1994), a keystone prey for vertebrate predators in the north-west Atlantic (e.g. Lavigne, 1996). These changes have been associated with population changes and with breeding failures of surface-feeding seabirds (Montevecchi and Tuck, 1987; Casey, 1994; Neuman, 1994; Regehr, 1995).

Seabirds are also influenced by fishery-induced changes (e.g. Howes and Montevecchi, 1993; Garthe *et al.*, 1996; Oro, 1996; Oro *et al.*, 1995), and both natural and anthropogenic perturbations have interactive influences on seabird feeding ecology and breeding biology (Montevecchi, 1993; Regehr and Montevecchi, 1997). Recent oceanographic and fishery-induced changes in seabird food supplies have had interactive effects in the north-west Atlantic. The influences of cold-water incursions on seabirds were compounded by the simultaneous closure of the groundfishery in eastern Canada in 1992. This closure resulted

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in a cessation of fishery offal discarding and thus cut off artificial food sources that helped support large populations of scavenging herring gulls (*Larus argentatus*) and great black-backed gulls (*L. marinus*). Decreased discarding in the 1990s coincided with breeding failures and population declines among large *Larus* gulls (Howes and Montevecchi, 1993; Montevecchi, 1996; H. M. Regehr and M. S. Rodway, unpublished data) and with intense predatory activity of gulls directed at other seabirds and their eggs and chicks (e.g. Russell and Montevecchi, 1996; Regehr and Montevecchi, 1997). Thus, the interactive effects of the unavailability of prey associated with cold sea surface temperature (SST) and intense predation pressures exerted by food-stressed herring and great black-backed gulls resulted in large-scale breeding failures of surface-feeding black-legged kittiwakes (*Rissa tridactyla*) in the north-west Atlantic (Regehr, 1995; Regehr and Montevecchi, 1997).

In this paper, we document a century-long trend of warming SST and an accompanying population increase of northern gannets (*Sula bassana*) that corresponds with increases in their primary prey, mackerel (*Scomber scombrus*). Mackerel is a lipid-rich fish that is a primary food for rapidly growing, lipid-loading gannet chicks (Montevecchi *et al.*, 1984). On a decadal time scale, anomalies in SST are analysed for concordance with changes in prey consumption by gannets during their breeding season when chick-feeding rates and, hence, energy demands are high.

Study sites and methods

Research was conducted off the north-east coast of Newfoundland on Funk Island (49°45′N 53°11′W), where the breeding population of gannets is 6000 + pairs (Nettleship and Chapdelaine, 1988) and the breeding population of common guillemots is ca. 400 000 pairs (Birkhead and Nettleship, 1980). Data on population trends of gannets are derived from sources in Montevecchi and Tuck (1987). Catches of mackerel were obtained from Fisheries and Oceans data files and are used as relative abundance indices. Annual SSTs during June and July were obtained from hydrographic station 27 (47°32.8′N 52°35.2′W), which is located 20 km east of St John's in the inshore branch of the Labrador Current and which was established in 1946. Ocean climate signals over the Newfoundland Shelf correlate well with temperature measurements at station 27 (Petrie *et al.*, 1988; Myers *et al.*, 1990). SST data from the ship of opportunity Comprehensive Oceanographic and Atmospheric Data Set (COADS) were used to extend the data series back to 1870. In order to reduce seasonal and inter-annual variation, decadal anomalies in SST were calculated for the northern Newfoundland Shelf for each decade from 1870 to 1990. Century-long series of September air temperatures from Godthåb, Greenland, and St John's, Newfoundland, were analysed because they were well correlated with SST during June and July. Air temperature data were smoothed with lowess smoothers (Cleveland, 1979), which involved 25-year intervals centred on each record, with nearby points weighted most heavily.

Data on seabird diets consist of the prey that adults delivered to chicks and that adults regurgitated at roosts. Prey samples were obtained from gannets by approaching birds at nests and at roosts, and identifying all prey samples and weighing fish prey samples regurgitated by adults and chicks. Approximately 7% (range 1–13%) of the regurgitations checked each year contained more than one prey species. Studies were conducted primarily during August and infrequently during July and September from 1977 to 1996, excluding 1981 when attempts to land on the island were unsuccessful. In total, 6551 prey samples were obtained from gannets. The frequencies of different prey species in the gannets' annual harvests were converted to biomass on the basis of the average masses of regurgitations of different prey: mackerel (377 g), Atlantic herring (*Clupea harengus*; 280 g), cod (*Gadus morhua*; 228 g), Atlantic salmon (*Salmo salar*; 177 g), capelin (*Mallotus villosus*; 156 g), short-finned squid (*Illex illecebrosus*; 149 g), Atlantic saury (*Scomberesox saurus*; 177 g), sandlance (*Ammodytes* spp.; 105 g). Nonparametric Kruskal-Wallis one-way analysis of variance (Siegel, 1957) was used to test for annual differences in the proportions of different species of prey consumed by gannets.

Results

Centurial warming of sea surface temperatures and gannet population growth

The SST anomalies from the 1870s to the 1990s indicate a general long-term warming trend with a decadally positive pulse in the 1930s through the 1950s (Fig. 1b). The September air temperature data from St John's and Godthåb are consistent with the SST trends indicating a large-scale climate warming during the same interval (Fig. 1c, d). The breeding population of northern gannets was at very low levels during the 19th century and absent during the early decades of the 20th century (Fig. 1a). The gannetry was re-established in the 1930s, and the number of pairs increased rapidly from the 1930s to the 1950s. These population trends corresponded closely with the fishery catches of mackerel in the region (Fig. 1a).

Decadal surface water anomalies and dietary shifts by gannets

Summer SSTs on the northern Newfoundland Shelf have varied by about 4°C during the past 50 years,

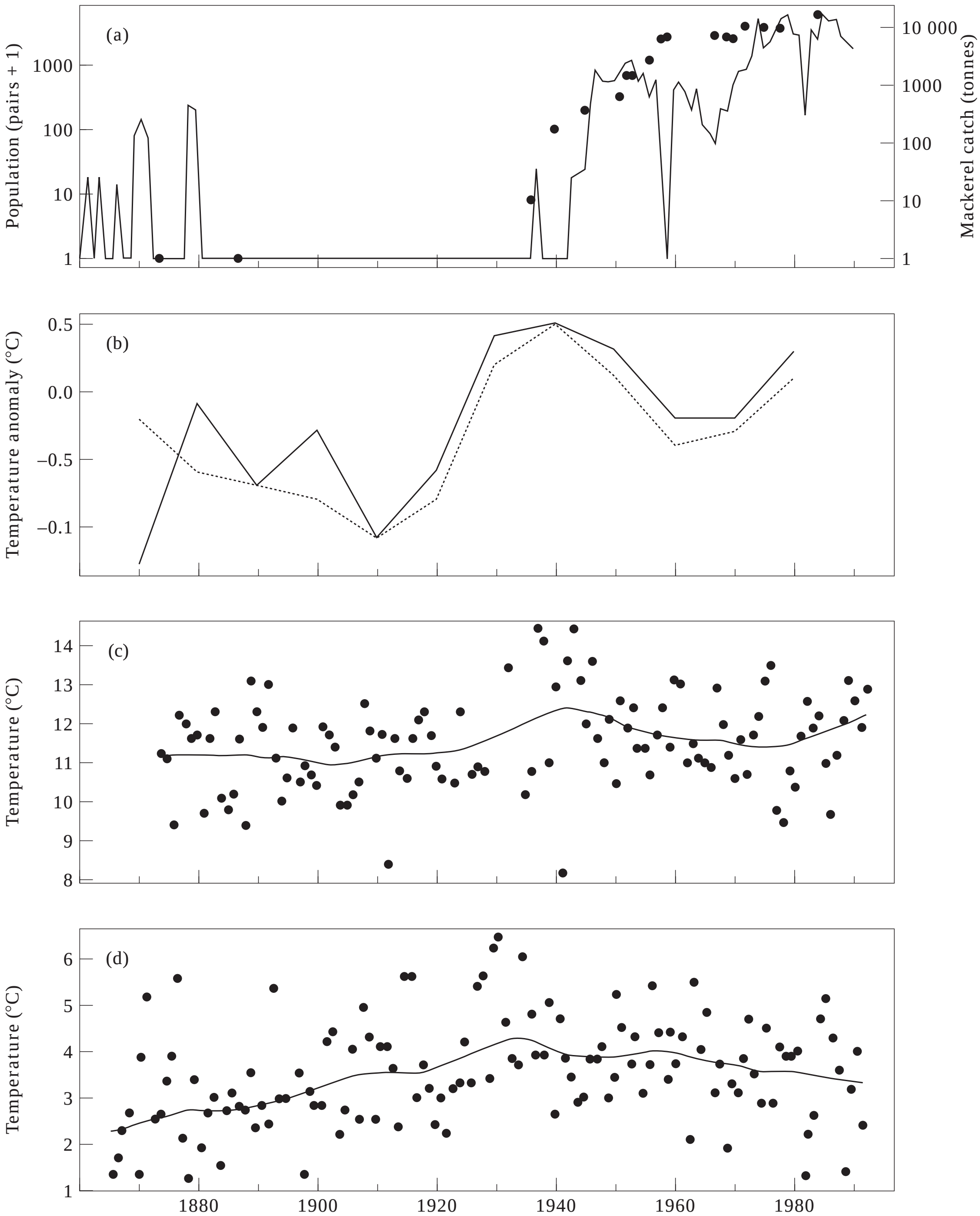

Figure 1. (a) Breeding population (pairs) of northern gannets (●) on Funk Island and catches of mackerel (——) in the Newfoundland region; (b) reconstructed sea surface temperatures (SST) anomalies over the north-east (——) and north-west (- - - -) Newfoundland Shelf during the late 19th and 20th century; corresponding air temperatures from (c) St John's, Newfoundland and (d) Godthåb, Greenland are given in the lower panels.

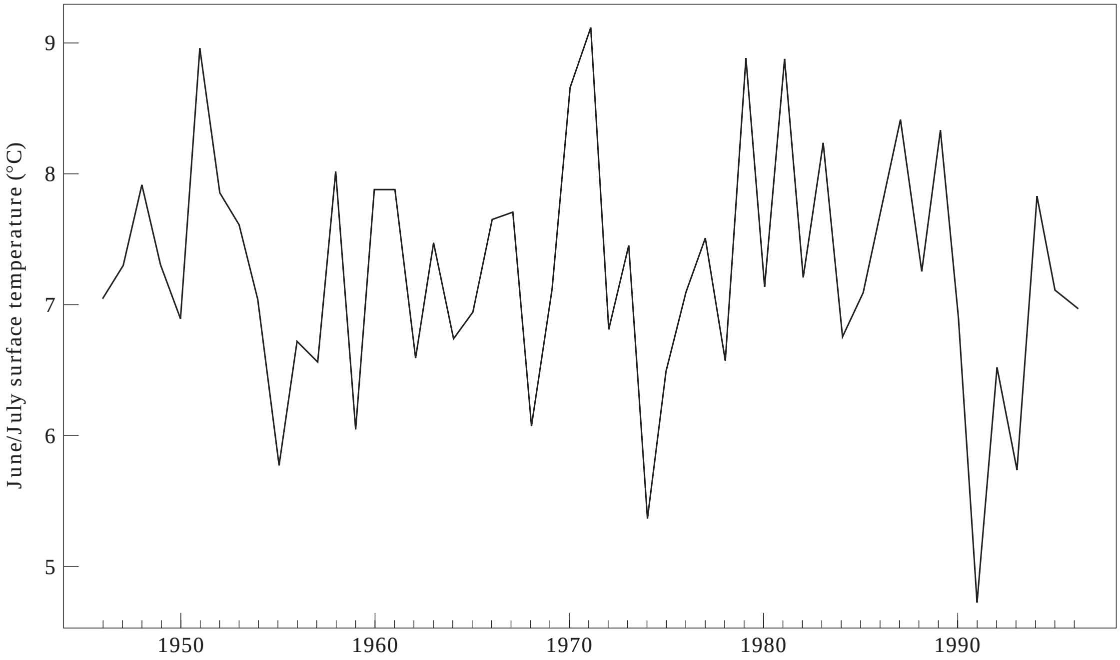

Figure 2. Summer sea surface temperatures (0–10 m) from hydrographic station 27 in inshore branch of the Labrador Current east of Newfoundland, 1946–1996.

showing sharp decreases in the mid-1950s, mid-1970s, and in the early 1990s (Fig. 2). The coldest late summer SSTs on record at hydrographic station 27 were made during 1991. SSTs returned to mean normal temperatures from 1994 to 1996 (Fig. 2).

The prey harvests of northern gannets on Funk Island varied considerably from 1977 to 1996 (Fig. 3). In the late 1970s and early 1980s, mackerel dominated the gannets' prey, except in 1982 when very few mackerel were taken. From 1989 to 1996, mackerel was a less significant component of the gannets' diet than it was from 1977 to 1988 ($H_1=7.62$, $p<0.01$; Fig. 3). Herring occurred in the diet in all years with largest harvests being shown in 1982, 1993, and 1994 (Fig. 3). Short-finned squid was a minor component of the diet from 1977 to 1982, essentially disappearing from the diet after 1983 with a slight showing in 1996 (Fig. 3). Atlantic saury were important prey in the mid- and late-1980s but not in other years. Capelin was the largest or a large contributor to the biomass of prey harvests from 1990 to 1996, but only in two years before this – 1978 and 1987 (Fig. 3). Evidence of Atlantic salmon and Atlantic cod was found in the diets in the 1990s.

The species taken by gannets may be classified into cold-water and migratory warm-water prey categories. Cold-water prey include capelin, herring, sandlance, salmon, and cod; migratory warm-water prey include mackerel, short-finned squid and saury. A striking shift in the annual proportions of prey harvests from mostly migratory warm-water before 1990 to mostly cold-water prey from 1990 to 1996 is evident ($H_1=7.86$, $p<0.01$; Fig. 4).

Discussion

Centurial warming of sea surface temperature and gannet population growth

The gannet colony on Funk Island was eliminated by human disturbance and exploitation in the 19th century (Montevecchi and Tuck, 1987). During the past century, SST and air temperatures in the north-west Atlantic have exhibited a gradual and widespread warming trend, with a marked increase during the 1930s, 1940s, and 1950s. Coincident with these trends, the gannet colony re-established in the 1930s and grew rapidly over the next three decades largely due to immigration (Montevecchi and Tuck, 1987). Associated increases of mackerel have been attributed to a slight warming of surface waters in the 1930s, 1940s, and 1950s. Presumably, slight increases in SST in the region allowed these migratory warm-water fish to move back into Newfoundland waters and provide the resource base for a fishery for mackerel to be prosecuted (Templeman and Fleming, 1953; Tuck, 1961).

Decadal surface water anomalies and dietary shifts by gannets

Within the century-long trend of warming surface waters in the north-west Atlantic, decadally anomalous

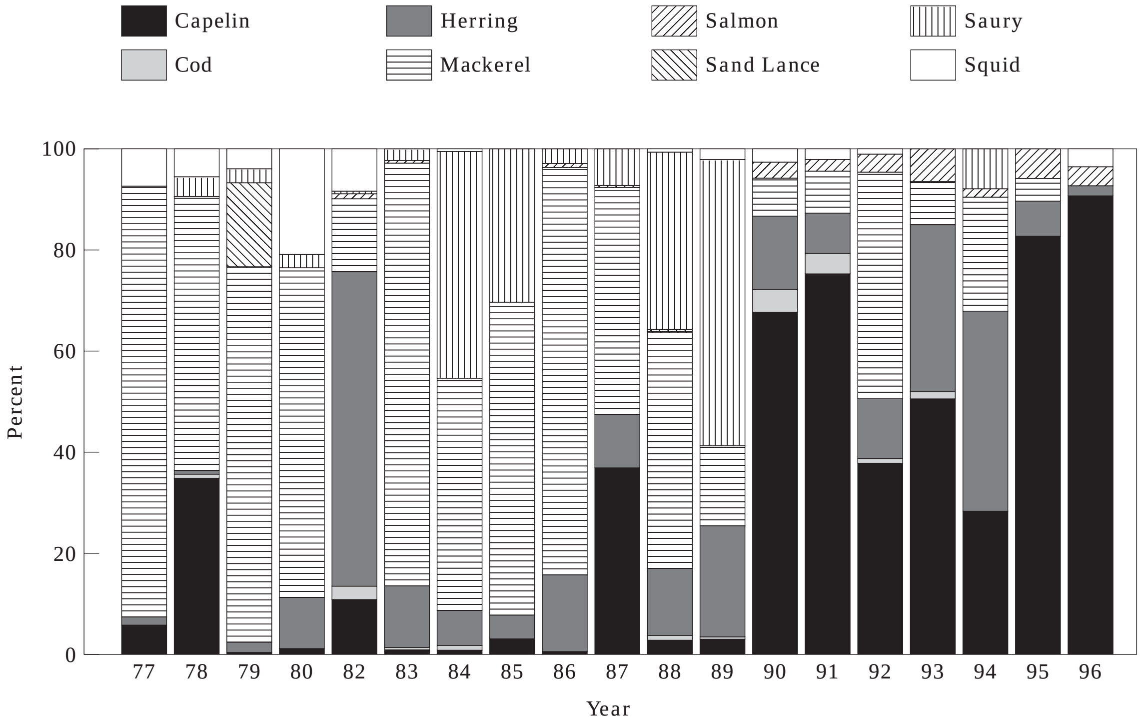

Figure 3. Annual percentages of total biomass of prey regurgitated by gannets on Funk Island, 1977–1996.

cold-water events occurred during the early 1990s. Gannets are opportunistic foragers and prey on abundant pelagic fish and squid. Inter-annual fluctuations in the proportions of mackerel and squid in their diets are highly correlated with local and regional fisheries catches and abundance indices of these prey in the north-west Atlantic (Montevecchi and Myers, 1995). During the 1990s, the gannets' prey harvests shifted from migratory warm-water pelagic fish and squid to regional cold-water pelagic fish. This dietary change reflected a shift in pelagic food webs on the Newfoundland Shelf (Montevecchi and Myers, 1996).

Cold SSTs in the 1990s presumably inhibited long-distance, migratory warm-water fish and squid from moving into the Newfoundland region (cf., Templeman and Fleming, 1953; Tuck, 1961). It should be emphasized, however, that relationships between fish behaviour and water temperature regimes are multi-dimensional and complex. For instance, the initial transition in the composition of the gannets' prey appeared in 1990 before the anomalous temperature decrease in SST in 1991, and mackerel consumption by gannets was low in 1982, when herring were a major prey item in chick diets and when surface water thermal regimes were not anomalous. It must also be noted that the virtual absence of short-finned squid from the diets of gannet chicks after 1983 was probably influenced by intense fishing pressure in the late 1970s and early 1980s (Montevecchi, 1993).

The recent prevalence of capelin in the gannets' diets in August is in large measure a consequence of the delayed inshore spawning movements of capelin in the 1990s. Capelin usually spawn in eastern Newfoundland in late June and July, but spawning has been delayed by three to six weeks in the 1990s (Shackell *et al.*, 1990; Nakashima, 1994, 1995). Moreover, surveys for capelin in the 1990s have found capelin to be locally concentrated in the area of the Funk Island Bank (J. E. Carscaddan, pers. comm.) within the foraging range of gannets from the colony on Funk Island.

Influences of oceanographic change on prey availability, trophic relationships, and seabird ecology

The examples presented in this paper are consistent in indicating that natural and anthropogenic perturbations have interactive and synergistic effects on fish distributions and populations and, hence, on seabird feeding ecology and reproductive success (e.g. Regehr and Montevecchi, 1997). It is also apparent that slight changes in ocean thermal regimes can induce profound changes in the temporal and spatial (both vertical and horizontal) distributions and migratory patterns of

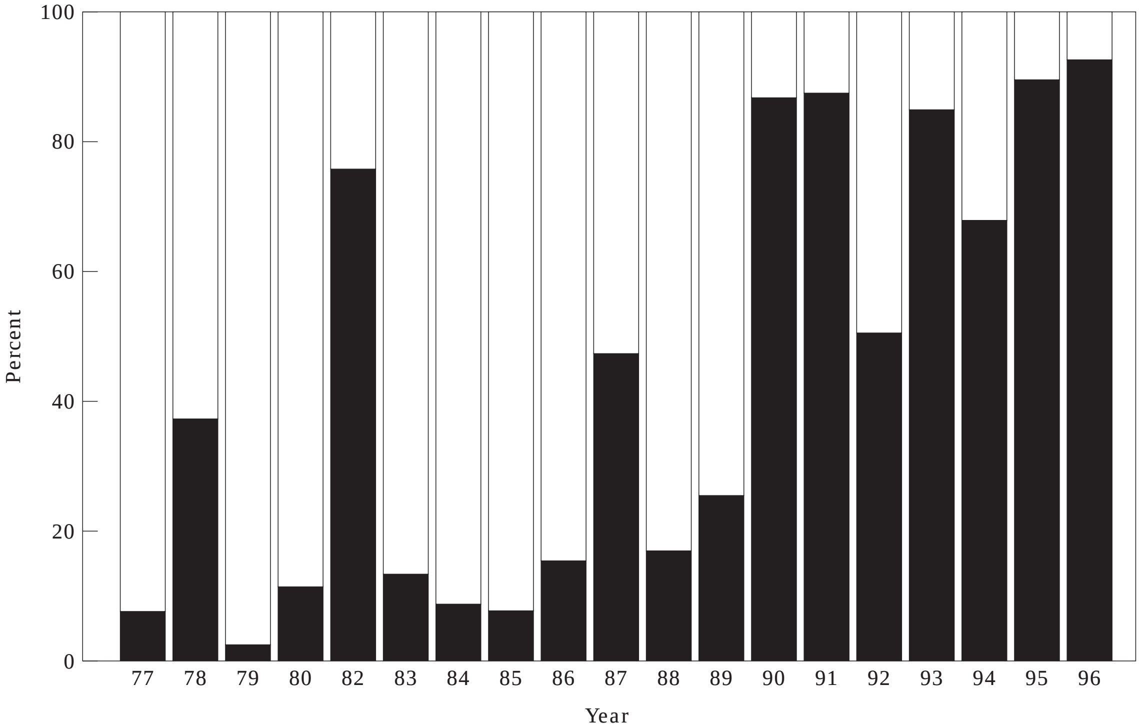

Figure 4. Annual percentage of total biomass of migratory warm-water prey (mackerel, Atlantic saury, short-finned squid in white) and cold-water prey (herring, capelin, Atlantic salmon, sandlance, cod in black) regurgitated by gannets on Funk Island, 1977–1996.

pelagic fish (e.g. Templeman and Fleming, 1953; Methvin and Piatt, 1991; Shackell *et al.*, 1990). Changes in prey distributions determine their availability to piscivorous and planktivorous seabirds. Such interactions imply that slight changes in oceanographic conditions associated with climatic warming might have large-scale and pervasive effects on vertebrate trophic interactions that could influence seabird reproductive success and population change. Furthermore, we might also expect to detect the initial influences of such oceanographic changes near the limits of seabird ranges (see Barrett and Krasnov, 1996) and most especially near the margins of oceanographic regions, such as the Newfoundland Shelf where low-arctic water makes its southernmost penetration.

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