DIETARY CHANGES OF SEABIRDS INDICATE SHIFTS IN PELAGIC FOOD WEBS

W.A. MONTEVECCHI & R.A. MYERS

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Long-term monitoring of prey deliveries to chicks by gannets and guillemots have provided useful indices of annual variability in the timing of the inshore movements, relative abundance, sizes and reproductive conditions of pelagic fishes and cephalopods in the Northwest Atlantic. From 1977 through 1994, prey harvests by gannets tended to shift from warm-water, long-distance migrants (mackerel, squid, saury) to cold-water residents (capelin). Annual variation in prey harvests by gannets and guillemots indicated 3- to 4-week delays in the inshore migration, reproductive maturation and spawning by capelin during cold sea surface events in the 1990s.

Cold surface water anomalies appear to have influenced pelagic food webs by inhibiting the movements of migrant, warm-water pelagic fishes and cephalopods into inshore regions in the Northwest Atlantic. These oceanographic influences may have amplified the effects of the overfishing of short-finned squid in the region in the late 1970s/early 1980s. We contrast recent effects of cold water perturbations on pelagic fishes with contentions about environmental influences on the demise of demersal cod in the Northwest Atlantic.

W. A. Montevecchi, Biopsychology Program, Memorial University of Newfoundland, St. John's, Newfoundland A1B 3X9, Canada. – R. A. Myers, Science Branch, Department of Fisheries and Oceans, P.O. Box 5667, St. John's, Newfoundland A1C 5X1, Canada.

INTRODUCTION

Most seabirds feed on small pelagic fishes, squids and crustaceans that occur in the upper and mid-water column and that are often important prey of large fishes and marine mammals (RICE 1992; MONTEVECCHI 1993a). Studies of prey harvests by seabirds provide natural indices of inter-annual fluctuations in prey abundance, availability and distribution (MONTEVECCHI & al. 1987; BAILEY & al. 1991; BOST & LEMAHO 1993; see also LILLY 1991). These indices can often be very informative because pelagic fishes, squids and crustaceans avoid vessels, are highly mobile, patchily distributed and difficult to assess (CLARKE 1977; STOBO & al. 1982), often occurring in the 'hydroacoustically invisible' upper water column (HAMPTON & al. 1979; DOMMASNES & ROTTIGEN 1985) and in inshore regions that are not surveyed (HEWITT & BREWER 1983; BERGSTAD & al. 1987; BARRETT & al. 1990). Moreover, indices based on catch and catch per unit effort (CPUE) data obtained from commercial vessels have been confounded with technical innovation in the locating and capturing of fish, with discarding, by-catches, misreporting, market demands, catch quotas, etc. (SHANNON & al. 1984; HARRIS 1990; MONTEVECCHI 1993a). Indices of pelagic fishes and cephalopods are needed, because these animals exhibit large interannual fluctuations in recruitment (SHELTON & al. 1985; BLACK & al. 1987; MYERS & al. 1995), and because fisheries directed at them tend to collapse (MACCALL 1979; MCEVOY 1986; LUDWIG & al. 1993). Seabirds also prey on fishes and invertebrates that are not exploited commercially and that hence receive minimal research attention. For these species, seabirds may provide the only available indices of abundance, occurrence and distribution (MONTEVECCHI & al. 1988; CROXALL 1989; BERTRAM & KAISER 1993; BOST & al. 1994; STEELE & MONTEVECCHI 1994).

Cold-water events in the Northwest Atlantic during the early 1990s, which were significantly anomalous on decadal time scales (DRINKWATER & al. 1994), influenced the timing, movement patterns and accessibility (by seabirds) of pelagic fishes and invertebrates (MONTEVECCHI & MYERS 1992). These cold-water perturbations had profound negative consequences on the reproductive success of surface feeding black-legged kittiwakes (*Rissa trydactyla,* LINNAEUS; CASEY 1994; NEUMAN 1994; REGEHR 1995).

The present study investigated and overviewed the influences of oceanographic conditions on the prey harvests of northern gannets (*Sula bassanus*, LINNAEUS) and common guillemots (*Uria aalge*, PONTOPPIDAN) at a large

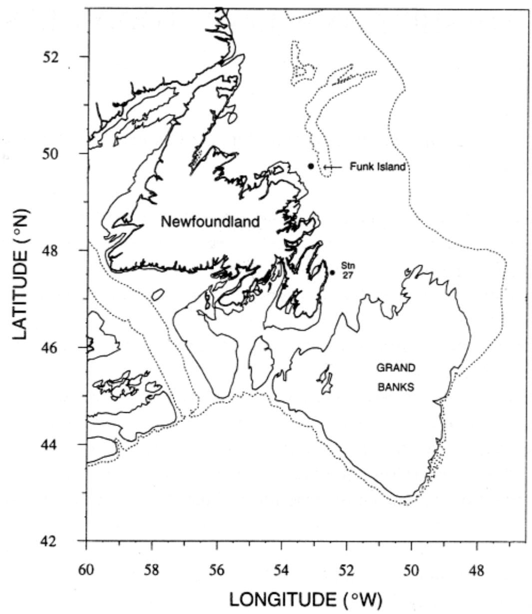

Fig. 1. Locations of Funk Island, hydrographic station 27 and the 100 m (light solid line) and 400 m (dashed line) isobaths.

seabird breeding community in the Northwest Atlantic. Here, gannet chicks are fed mackerel (*Scomber scombrus*, LINNAEUS) short-finned squid (*Illex illecebrosus*, LESUEUER), Atlantic herring (*Clupea harengus*, LINNAEUS), capelin (*Mallotus villosus*, MULLER) and Atlantic saury (*Scomberesox saurus*, WALBAUM), and guillemot chicks are fed capelin almost exclusively. All of these prey species have been exploited commercially in the Northwest Atlantic. Capelin is more generally a primary prey of large vertebrate food webs in the Northwest Atlantic, e.g. cod (LILLY 1991), marine mammals (CARSCADDEN 1984; WHITEHEAD & CARSCADDEN 1985) and birds (BROWN & NETTLESHIP 1984; CAIRNS & al. 1986), and successful reproduction by many seabird species in the Northwest Atlantic depends on the availability and timing of the inshore movements of capelin (see also VADER & al. 1990). The present study used long-term (18-year) and recently established (5-year) food sampling programs directed at gannets and guillemots to assess associations of inter-annual fluctuations in seabird prey harvests with changes in oceanographic conditions. Changing patterns of seabird prey harvests are used to infer shifts in pelagic food webs.

METHODS

Data on the population growth of the gannet and guillemot colonies on Funk Island (49° 45' N, 53° 11' W) off the northeast coast of Newfoundland (Fig. 1) are derived from sources in MONTEVECCHI & TUCK (1987). From 1977 through 1994, 4785 food samples were collected during August, with a small number collected in July and September (see MONTEVECCHI & MYERS 1995) in the gannet colony of 6,000+ breeding pairs, on Funk Island (NETTLESHIP & CHAPDELAINE 1988). Numbers of samples in each year ranged from 48 to 498 with a median of 252. Gannets regurgitate food to chicks, and adults and chicks often regurgitate at the approach of a researcher. Samples were obtained by approaching birds in the colony and at roosts. Food samples obtained from adults were often fresh, i.e., eyes intact, and almost always identifiable to species. From 1990 through 1994, 460 food samples were obtained from guillemots by using dip nets attached to poles to capture birds carrying prey as they flew into the colony. Fresh food samples were weighed with Pesola spring scales, and their fork, total and/or mantel lengths recorded. The frequencies of prey in the gannets' annual harvests were converted to biomass on the basis of the mean masses of fresh prey items (MONTEVECCHI & MYERS 1992; MONTEVECCHI & al. 1987). The fork and total lengths, masses, genders and reproductive statuses (gravid, spent, immature) were recorded for fresh capelin collected from gannets and guillemots and were compared for 1990 through 1994, years when gannets landed high percentages of capelin.

The three longest time series of temperature data were examined. Air temperature records from St. John's, Newfoundland and from Godthåb, Greenland extend back to the 19 century. We examined September air temperatures in St. John's because they were well correlated with sea surface temperatures (SST) in September ($r = 0.54$, $n = 44$, $p < 0.001$), the month that mackerel and squid are most abundant in Newfoundland waters. This record was augmented with the Godthåb series. SST data from the ship of opportunity Comprehensive Oceanographic and Atmospheric Data Set (COADS) were used to extend the time series back to 1870. Decadal anomalies were calculated for the northern Grand Banks for each decade from 1870 through the 1990s. SSTs and salinity (0-10 m) for different months were obtained from hydrographic station 27 (47° 32.8' N, 52° 35.2' W), which was established in 1946, and is located 20 km east of St. John's in the inshore branch of the Labrador Current. Station 27 has been attended by research vessels entering and leaving St. John's Harbour, approximately twice monthly since 1950. Temperature and salinity measurements from station 27 are highly correlated with data collected at moorings and cross shelf transects from Hamilton Bank off southern Labrador to the northern Grand Banks, and PETRIE & al. (1988) concluded that ocean climate signals over the entire region (see Fig. 1) were well represented by station 27 (MYERS & al. 1988, 1990). Correlation were run between average SSTs (for June and July) and percentages by mass of capelin landed by gannets on Funk Island from 1977 through 1994.

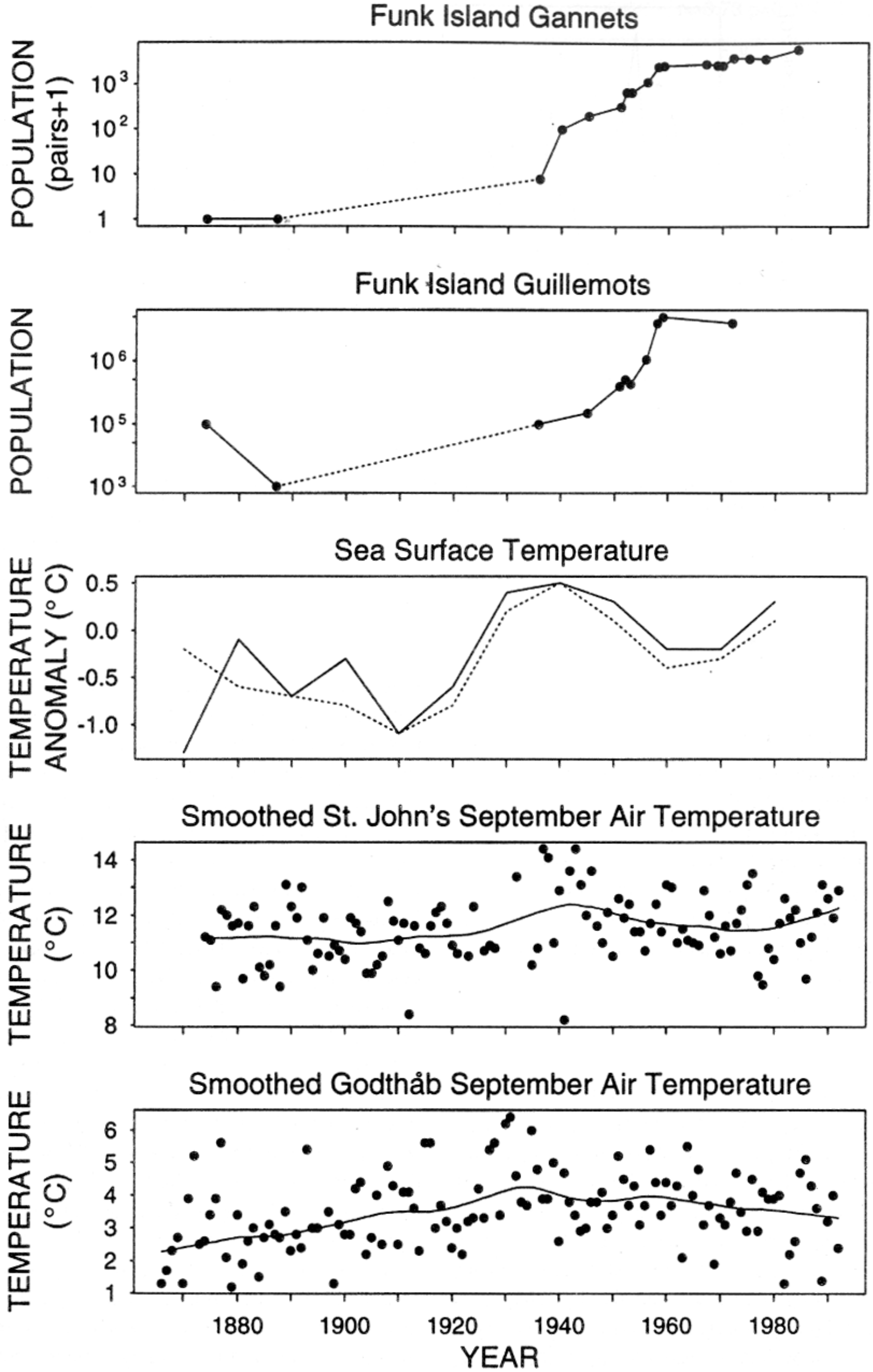

Fig. 2. Re-establishment of the gannetry and growth of the colonies (breeding pairs) of gannets and guillemots on Funk Island during the 19th and 20th centuries, and reconstructed sea surface temperature [SST] patterns over the Northeast and Northwest Grand Banks, and September air temperatures from St. John's, Newfoundland and Godthåb, Greenland. The air temperature data were smoothed using lowess smoothers, robust locally weighted regressions (Cleveland 1979). A window, in our case of 25 years, is placed about each observation; points that are inside the window are weighted so that nearby points get the most weight.

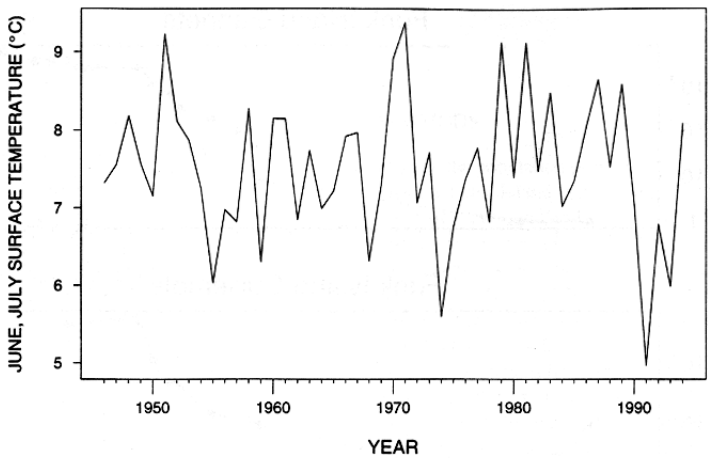

Fig. 3. Sea surface (0-10m) temperatures recorded at hydrographic station 27 from 1946-1994.

RESULTS

Growth of the gannet and guillemot colonies

Following extirpation in the 19 century, the gannet colony was re-established on Funk Island in the 1930s. In recent decades the colonies of both gannets and guillemots have grown substantially, at rates that would require immigration to generate them. These events corresponded with a general increase in SST and air temperatures in the Northwest Atlantic during the 1930s and 1940s (Fig. 2).

Sea surface thermal trends

During the past 50 years, SST has varied by about 4° C during June and July off northeastern Newfoundland (NAFO Divisions 3KL) with a sharp decrease during the early 1990s. The coldest SST on record at hydrographic station 27 was documented in 1991, and relatively warm SSTs were recorded in 1994 (Fig. 3). A general warming trend in the Northwest Atlantic during the past century has been reviewed by HUTCHINGS & MYERS (1995) who documented increases in ocean temperatures at 100 m on the Grand Bank, increases in sea ice cover from 1800, and concurrent trends in data from ground boreholes and from tree rings.

Inter-annual variation in prey harvests

Mackerel was the dominant prey that gannets delivered to chicks on Funk Island from 1977 through 1987, with the exception of 1982. In recent years (1988-1994), mackerel was not the most common prey delivered to chicks. Commercial fisheries for mackerel were extremely poor in all years when gannets showed low landings of mackerel (MONTEVECCHI & MYERS 1992; MONTEVECCHI 1993b). Short-finned squid, Atlantic saury and herring were delivered to chicks in lesser proportions, and herring dominated prey harvests in 1982, when little mackerel was landed. Squid were absent from or insignificant components of prey harvests after 1982, and commercial fisheries for squid failed completely during the period, 1983-1994 (MONTEVECCHI & MYERS 1992, 1995; MONTEVECCHI 1993b). Atlantic saury were important foods for gannet chicks in 1984, 1985, 1987, 1988, and were the most common prey fed to chicks in 1989. No saury were delivered to chicks from 1990 through 1993, though they were landed during 1994, when SST was warmer than during previous years in the 1990s. Capelin was the most common prey delivered to gannet chicks during August sampling periods during the 1990s. Atlantic salmon (*Salmo salar*, LINNAEUS) and small cod (*Gadus morhua*, LINNAEUS) were minor components of diet. Overall, the prey harvests of gannets increased in diversity through the 16-year sampling period, and the gannets' prey harvests have changed markedly since 1989.

The landings of capelin by gannets on Funk Island were highly inversely correlated with SST in June and July ($r = -0.73$, $n = 17$, $P < 0.001$, Fig. 4). Even though gannets are three times heavier than guillemots (~ 3.2 vs ~ 1 kg), both species landed the same-sized capelin at the same time in different years. For example in 1990, both species landed capelin that averaged 148 mm in total length, and in 1991, both species landed capelin that averaged 162 mm in total length. Guillemots and gannets, however, differed markedly in the proportions of male and female capelin that they delivered to chicks. Guillemots landed almost all female capelin in all years, whereas gannets landed relatively similar proportions of female and male capelin. Unexpectedly, the capelin landed by guillemots (Fig. 5; and gannets) were significantly longer ($F_{4,455}$ = 10.84, P < 0.001) and heavier ($F_{4,397}$ = 13.02, P < 0.001) in 1991 than in other years.

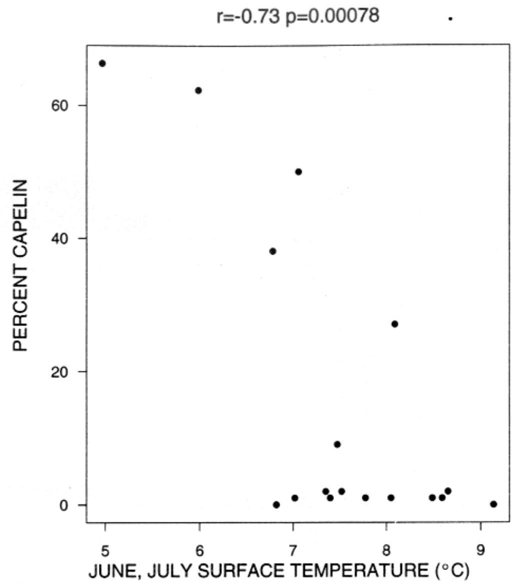

Fig. 4. The relationship between percentage mass of capelin in the prey harvests of gannets on Funk Island and average SSTs at station 27 in June and July from 1977 through 1994.

DISCUSSION

Growth of the gannet and guillemot colonies

The gannet and guillemot colonies and those of most other seabirds on Funk Island and elsewhere in the Northwest Atlantic were extirpated or severely reduced by human over exploitation and disturbance in the 19th century (Montevecchi & Tuck 1987). The re-establishment and growth of the gannet colony has been attributed to a warming of SST in the 1930s and 1940s which allowed mackerel to make a more northerly migration into Newfoundland waters (Templeman & Fleming 1953; Tuck 1961). We concur that these associations are striking. During the 1930s, 1940s, and 1950s, populations of gannets and guillemots on Funk Island exhibited exponential increases driven by immigration (Montevecchi & Tuck 1987). However, both species, but most especially the guillemots, also benefited from decreasing spring and summer hunting and disturbance pressures through these decades. At present we cannot differentiate environmental and anthropogenic influences on the growth of seabird populations during the 1930s through 1950s, but recognize that such effects may well have been interactive.

Inter-annual variation in prey harvests and sea surface temperature

From 1977 through 1994, gannets exhibited marked changes in the foods delivered to chicks at Funk Island during late summer. Mackerel was the most important food except in 1982 and in all years after 1988. The gannets' harvests of mackerel and squid corresponded significantly with fishery catches of mackerel over local, meso- and meta-spatial scales and over monthly and annual intervals in the Northwest Atlantic (Montevecchi & Myers 1992, 1995). The catch of mackerel in the Newfoundland region and elsewhere is only a small portion of their total population and is presumed to have little impact on the population (Anderson & Pagiorkowski 1980).

Squid, like mackerel, form dense surface schools and are probably easily located and captured by gannets. Short-finned squid was an important food of gannet chicks until 1983, when they virtually disappeared from the diet. Since 1983, the commercial fishery for short-finned squid in the Northwest Atlantic has failed completely. Fishing pressures in the late 1970s/early 1980s, stimulated by new Asian markets, probably produced or very greatly influenced the subsequent decline of short-finned squid in the Northwest Atlantic (Montevecchi 1993b). Harvests of squid increased from less than 500 tonnes/year in the 1960s to more than 160,000 tonnes in 1979 (Black & al. 1987). Large scale shifts in trophic relationships have been produced by fisheries activities in other oceanographic regions (Burger & Cooper 1984; Klages & al. 1992; Crawford & Dyer 1995). Cold surface water temperatures in the 1990s may have amplified the effects of these fishing pressures (e.g. Steele & Henderson 1984; Montevecchi 1993b).

During the mid to late 1980s, Atlantic saury, a long-distance migratory, warm-water pelagic fish (Dudnik & al. 1981; Montevecchi & Berutti 1991), comprised significant proportions of the diets fed to gannet chicks on Funk Island. However, these long-distance, migratory, warm-water pelagic fishes disappeared from the gannets' diets during the early 1990s, reoccurring during 1994

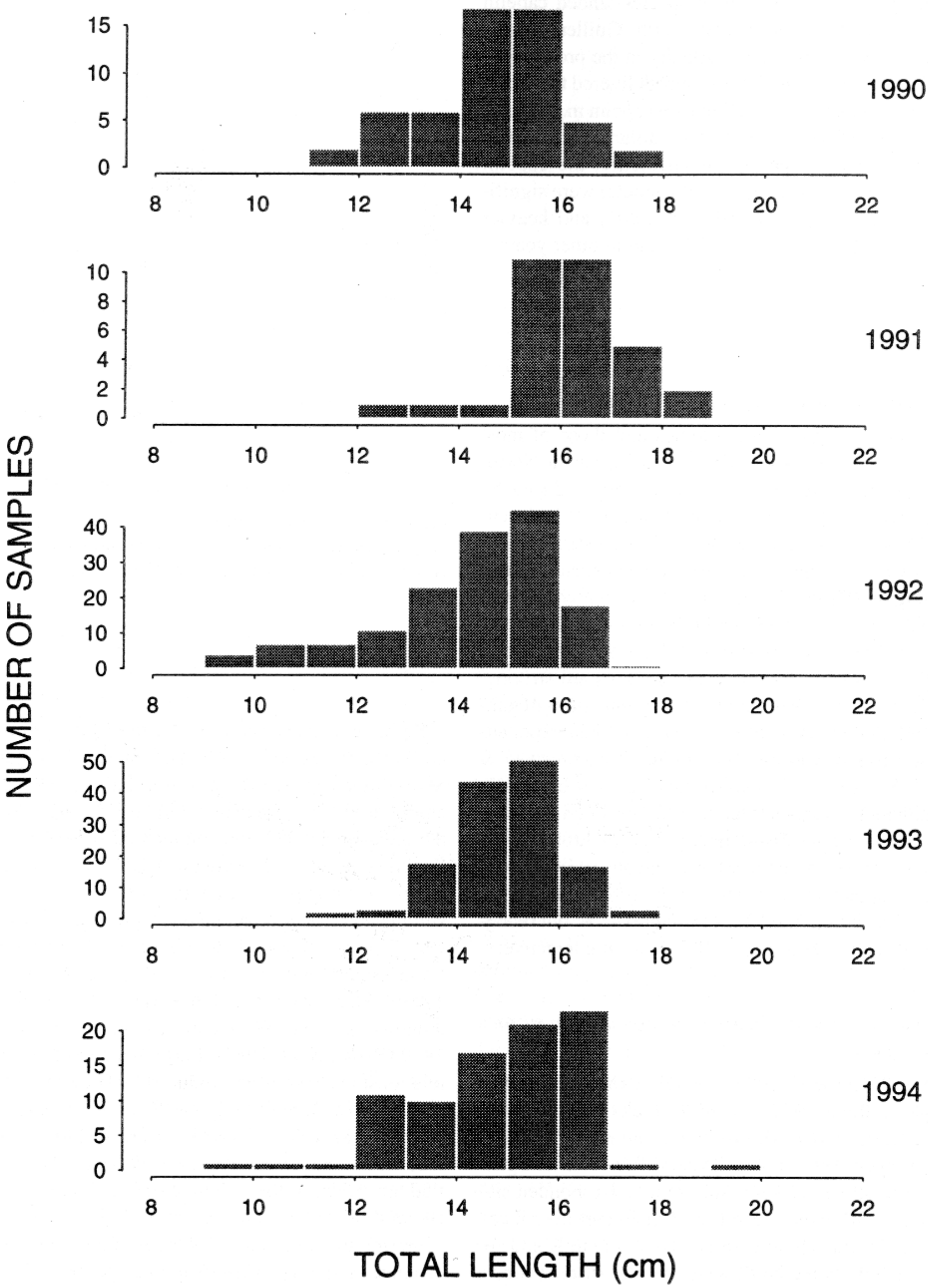

Fig. 5. Total length distributions of capelin delivered to guillemot chicks on Funk Island during August, 1990-1994.

when SSTs were high. Herring were important prey for gannets in 1982, when mackerel were in very low abundance in the region, and were less important components of chick diet in most other years. Salmon and cod were taken in small proportions.

We interpret these and other dietary changes of gannets during the late 1970s, 1980s, and early 1990s as indications of shifts in pelagic food webs on the northern Newfoundland Shelf. The overall pattern of prey harvests by gannets during this period suggests a shift away from an assemblage of warm-water pelagic prey (e.g. mackerel, squid, Atlantic saury) to colder water prey, consisting primarily of capelin. These changes in the proportions of cold- and warm-water pelagic prey delivered to gannet chicks on Funk Island correspond with cold SSTs during the 1990s. We are currently studying the temporal duration of these shifts in pelagic prey harvests. Highly migratory warm-water pelagic species, such as mackerel, squid and Atlantic saury, apparently did not move into the Northwest Atlantic in abundance during the 1990s, owing at least in part to cold surface water events (MONTEVECCHI & MYERS 1995). Gannets nesting on Funk Island are probably very greatly influenced by changes in oceanographic conditions because this colony lies at the northern limit of the species' breeding range in the Northwest Atlantic, and because Funk Island is situated in the coldest water of any gannet colony in the world.

Cold water-induced dietary changes and breeding success

While the gannets' breeding success did not appear to be adversely affected by these dietary shifts, surface-feeding black-legged kittiwakes exhibited very poor production in the Northwest Atlantic during the early 1990s (CASEY 1994; NEUMAN 1994; REGEHR 1995). Some of this poor production is due to increased predation pressure by great black-backed gulls (*Larus marinus*, LINNAEUS) and herring gulls (*L. argentatus,* PONTOPPIDAN; REGEHR 1995) that have lost access to massive tonnages of fish offal following fishery closures in eastern Newfoundland in 1992 (see HOWES & MONTEVECCHI 1993). Guillemots and Atlantic puffins (*Fratercula arctica*, LINNAEUS) that prey primarily on capelin in the Northwest Atlantic, showed substantially delayed breeding chronologies during 1990s (see RODWAY 1995), the consequences of which are unknown but most probably reduce production.

Comparison of capelin harvests by gannets and guillemots

Gannets are three times heavier than common guillemots and forage nearer the surface, yet both species delivered the same-sized capelin to their chicks in different years. Although such a finding may suggest an unselective sampling of available prey by different seabird species, marked differences in other characteristics of the capelin delivered to chicks by guillemots and gannets were evident. Gannets delivered relatively similar proportions of male and female capelin, while guillemots fed almost exclusively female capelin (high proportions of which were gravid in some years) to chicks (MONTEVECCHI & MYERS, own obs.). During spawning periods, schools of female capelin tend to occur higher in the water column than schools of male capelin, and it has been suggested that females are more accessible to pursuit-diving guillemots (ERIKSTAD & VADER 1989). However, the high proportions of male capelin in the prey harvests of gannets clearly indicate that male capelin were accessible to guillemots. These circumstances suggest that guillemots either actively select or find it easier to capture female capelin. The energy densities of gravid capelin are higher than those of spent females or male capelin (MONTEVECCHI & PIATT 1984), so the delivery of high proportions of gravid female capelin to chicks might indicate that guillemots are foraging optimally. Studies of the behaviour of individual avian predators and fine scale distributions of their prey are needed to differentiate alternative foraging strategies. Yet whatever the case from a behavioural standpoint, the relatively exclusive predation by guillemots on female capelin will greatly influence the consequences on local capelin populations (see BROWN & NETTLESHIP 1984; CARSCADDEN 1984; CAIRNS & al. 1986, 1990) and needs to be taken into account in large scale energetic models (e.g. DIAMOND & al. 1993; BARRETT & al. 1994).

Cold water and pelagic and demersal fishes

Cold water influences also delayed the inshore migration, maturation and spawning of capelin by about 3-4 weeks in the 1990s (SHACKELL & al. 1990; NAKASHIMA 1994). This delay made capelin available to gannets in August, by which time they would have usually moved back offshore and lower in the water column after spawning and out of the range of breeding gannets attached to inshore colonies. During summer 1991, when the SST was the coldest on record in the Northwest Atlantic and capelin arrived latest, the capelin landed by both guillemots and gannets were significantly larger than in other years. As the mean length-at-age of capelin declined in the 1990s, and as large capelin tend to move inshore before smaller younger ones (NAKASHIMA 1994), this finding probably reflects the late migratory chronology of capelin during 1991.

HUTCHINGS & MYERS (1994) also documented similar delays in the spawning of cod on the northern Grand Bank during cold water periods. We emphasize, however, that while the present findings of cold-water induced shifts in pelagic foods webs appear consistent with contentions about the influences of cold water events on the recent collapse of cod in the Northwest Atlantic, the generalization is not valid. The demise of the cod is attributable to overfishing with no detectable influence of cold water on population dynamics other than a change in the timing of spawning (HUTCHINGS & MYERS 1995) or a reduction in growth rate (MILLAR & MYERS 1990). It is clear that anthropogenic and environmental effects on fish populations can be interactive, but it is also clear that the effects of cold water events on pelagic and demersal fish species and food webs are not generalizable.

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