

Prey harvests of seabirds reflect pelagic fish and squid abundance on multiple spatial and temporal scales

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ABSTRACT: Many studies have demonstrated relationships between seabird prey harvests and fisheries catches. These correlations have for the most part been found at scales from 10s to 100s of kilometers within foraging ranges around seabird breeding colonies. In the present study, we investigated associations between the prey harvests of northern gannets *Sula bassana* at a large breeding colony off the northeast coast of Newfoundland and the catches of the inshore Newfoundland fishery at different spatial scales and time intervals. Significant correlations occurred between the seabirds' and the humans' catches of mackerel *Scomber scombrus* and short-finned squid *Illex illecebrosus* from 1977 through 1992. The relationships for squid were stronger over larger geographic areas than were those for mackerel. The associations for both squid and mackerel reflected abundance/availability around the colony, at a larger scale near the gannets' maximum foraging range (e.g. ~200 km), and for the entire Newfoundland region (1000s of kilometers). These correlations were significant at August vs August and August vs annual time intervals. The gannets' landings of squid were also associated with fishery-independent, research survey indices of squid abundance over thousands of kilometers. The robustness of these relationships indicates that levels of pelagic prey harvest by seabirds can provide reliable indices of prey abundance within and outside reproductive seasons and foraging ranges around breeding colonies. Similar relationships are predicted between seabird and human fisheries that are directed at migratory 'warm-water' pelagic prey that move into cold and high latitude oceanographic regions.

KEY WORDS: Bio-indication · Pelagic food webs · Seabirds · Trophic relationships

INTRODUCTION

Owing to patchy distributions and high mobility, it is difficult to survey and to estimate accurately abundances of pelagic fishes and invertebrates (e.g. Clarke 1977, Stobo et al. 1982). Fishery-independent estimates of the abundances of pelagic organisms based on acoustic, egg and larval surveys are rare and relatively unreliable (e.g. Hurley 1980a, Dawe & Beck 1985). Even when it is possible to locate pelagic prey on surveys, the schools of many species occur in 'hydroacoustically invisible' surface waters and also avoid ships (Diner & Masse 1987).

Dietary, energetics, behavioural and production data collected from seabirds have been used to derive

indices of prey abundance that can be incorporated into multi-species assessment models (e.g. Croxall 1989, Monaghan et al. 1989, Barrett et al. 1990, Bailey et al. 1991, Hatch & Sanger 1992, Montevecchi 1993, see also Lilly 1991). Interannual variation in the abundances of pelagic fishes and squids is often reflected in the prey harvests of seabirds (e.g. Hislop & Harris 1985, Montevecchi et al. 1987). Typically, these relationships are assumed to exist within avian foraging ranges around breeding colonies on scales of 10s to 100s of kilometres (Hunt et al. 1991). However, correlations between local prey harvests by seabirds at breeding colonies and large-scale variation in pelagic fish abundance indices have been reported. For example, parental food harvests by Atlantic puffins *Frater-*

cula arctica on the Isle of May (Scotland) have been shown to be strongly correlated with larval indices and abundances of herring *Clupea harengus* and sprats *Sprattus sprattus* in the North Sea (Hislop & Harris 1985). Relationships like these can be used to monitor the abundance of pelagic fishes. Such bio-assays will be more useful if the prey harvests of seabirds reflect more than local, transitory fluctuations in prey populations (Hunt et al. 1991).

The prey harvests of northern gannets *Sula bassana* and cape gannets *S. capensis* are known to correlate with inter-annual meso-scale (10^2 km) fluctuations in fisheries catches of pelagic fishes and squids (Montevecchi et al. 1987, Montevecchi & Berruti 1991, Klages et al. 1992). In the present paper, we examine the spatial and temporal relationships between fisheries and seabird catches of mackerel *Scomber scombrus* and short-finned squid *Illex illecebrosus*. Both mackerel and squid are 'warm-water' pelagic species that migrate into the Northwest Atlantic during summer, when they are primary prey of breeding gannets (Montevecchi et al. 1984). Fishery catches of these species in the Newfoundland region occur mainly in late summer and early autumn. We compare a 15 yr data set of the landings of mackerel and squid by gannets during August in a large colony 60 km off the northeast coast of Newfoundland, Canada, to fisheries catches of these species during August and during annual intervals on spatial scales of 10s to 1000s of kilometres. We also compare squid landings by gannets with fishery-independent indices of the abundance of squid to assess if seabird data reflected abundance as well as availability to birds and fishermen.

METHODS

From 1977 through 1992, a total of 4474 food samples were collected during August (and rarely during July; Table 1) from gannets in the colony on Funk Island ($49^{\circ} 45' N$, $53 11' W$; Fig. 1, see Montevecchi & Tuck 1987). Food samples were obtained by approaching birds in the colony and at roosts. Gannets regurgitate food to chicks and often regurgitate loads at the approach of a researcher and before fleeing. Chicks behave similarly. Samples obtained from adults were often fresh, i.e. eyes intact, and almost always identifiable to species in the field. Fresh samples were weighed with Pesola spring scales, and their fork, total and/or mantle lengths measured. The frequencies of prey in the landings by gannets were converted to biomass on the basis of the mean masses of fresh prey items. Comparisons were made using Spearman rank-order correlations and Pearson product-moment correlations of the percentages of biomass [$\log(\% \text{ catch} + 1)$] of differ-

ent prey with the tonnages of commercial catches [$\log(\text{catch} + 1)$] during August and for entire years.

Data of fishery catches in different NAFO (Northwest Atlantic Fisheries Organization) areas and sub-areas were obtained from the Statistics Branch, Department of Fisheries and Oceans, St. John's, NF. Equivalent data do not exist for the other major prey species. In the Newfoundland region, neither mackerel nor squid have been under effective quota regulation, whereas capelin *Mallotus villosus* and herring *Clupea harengus* are under quota regulation. There is no commercial fishery for Atlantic saury *Scomberesox saurus*.

Inshore commercial catch probably provides a reasonable index of the level of mackerel and squid abundance for each subarea for which there is a substantial fishery (see Black et al. 1987), even though commercial catch is rarely a linear function of actual abundance and is heavily influenced by market demands. There has been a relatively constant number of fishermen in the pelagic fishery during the period of study, i.e. the number of full-time fishermen in Newfoundland from 1981 to 1992 varied from a minimum of 13 351 to a maximum of 14 619 (Donahue 1993). The main source of nonlinearity is likely that at high harvest levels, when catch is limited by the saturation of markets and processing capacity of fish plants.

We also considered estimates of the abundance of squid derived from research surveys to determine if the gannet harvest reflected prey abundance, and not only prey availability to birds and fishermen. We derived estimates of squid abundance from research surveys using bottom trawl gear designed to estimate

Table 1. Dates of collections and numbers of food samples collected from northern gannets *Sula bassana* on Funk Island, off Newfoundland, Canada

Year	Dates	No. of samples
1977	Jul 12	105
1978	Aug 11-20	241
1979	Jul 31 - Aug 6	163
1980	Aug 1-13	219
1982	Aug 9-13	196
1983	Aug 5-13	498
1984	Aug 9-19	289
1985	Aug 4-10	184
1986	Aug 7-15	494
1987	Aug 22-26	145
1988	Aug 12-20	525
1989	Aug 21-26	379
1990	Jul 18, 31 - Aug 11	341
1991	Aug 12-16	406
1992	Aug 5-10	289
1977-1992		4474

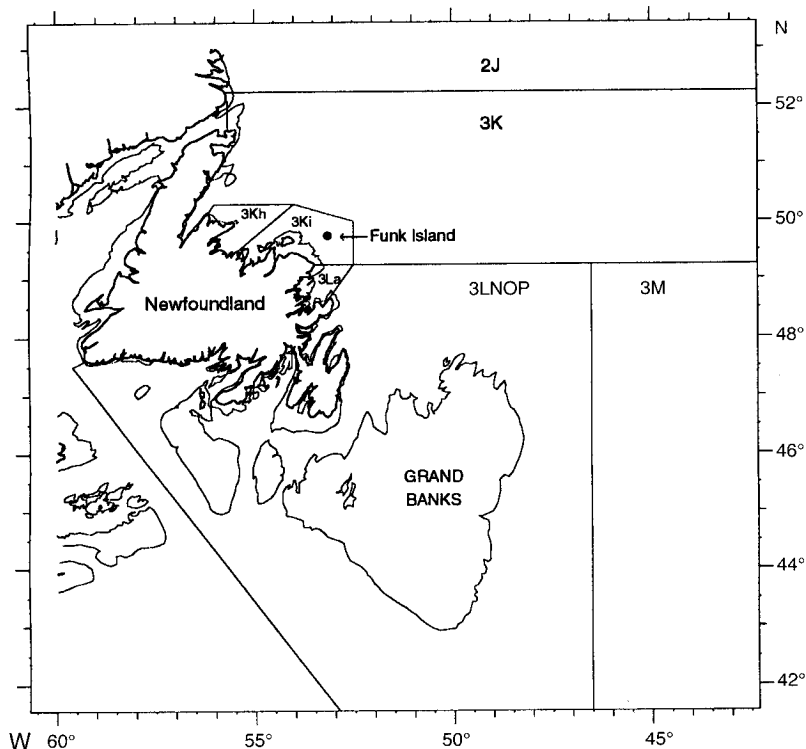


Fig. 1. Location of Funk Island and NAFO fisheries areas from which commercial catches of squid *Illex illecebrosus* and mackerel *Scomber scombrus* are compared with the prey landings of gannets *Sula bassana*. 3Ki = Funk Island Region; 3Kh, 3Ki, 3La = NE Newfoundland; 2J, 3K to 3P = Newfoundland Region. The 100 m isobath is also shown

groundfish abundance. These survey trawls catch squid incidentally. Furthermore, the surveys in the northern part of the Newfoundland region (NAFO Divisions 2J, 3K, 3L) take place later than the period of maximum squid abundance, i.e. in October and November. The surveys in the other Newfoundland regions (NAFO Divs. 3N, 3O, 3P) occur during spring before the period of maximum squid abundance [see Hutchings et al. (1993) for a description of these surveys]. We also used summer groundfish surveys on the Scotian Shelf (NAFO Divs. 4X, 4W, 4VN, 4VS). These use a different trawling gear that appears to be better at capturing squid (Doubleday & Rivard 1981). The mean number of squid caught per tow on these surveys was used as an index of abundance for the Scotian Shelf. Overall, we generated abundance indices for each of the 10 NAFO divisions listed above (see Table 2). We were unable to find or generate any fishery-independent estimates of the abundance of mackerel.

Two approaches were used to examine the spatial scale over which gannet diet was providing information on relative abundance of prey. First, we correlated gannet landings at Funk Island with commercial catch at 12 coastal fishing zones around insular Newfound-

land. We determined the region over which the correlation of gannet harvest at Funk Island was homogeneous, i.e. we asked if the correlations could be considered as samples from a population exhibiting a common correlation (Sokal & Rohlf 1981, p. 587). If we could reject the hypothesis of no heterogeneity among the correlation coefficients, we then determined which correlations were different from the 'local correlation', i.e. the correlation of gannet landings at Funk Island with the local catch from Div. 3Ki (Fig. 1). A significance level of 0.05 was used. We examined all statistical subdivisions from Labrador around the coast of Newfoundland to the southwest tip of the island. The catches of squid and mackerel in Labrador and the southwest region of Newfoundland were too small to yield reliable correlations, e.g. there were fewer than 6 years in which squid and mackerel were caught. All other subdivisions were used in analyses.

The second approach we used was to combine commercial catch data over 3 spatial scales: (1) the colony vicinity (Funk Island region: Div. 3Ki), (2) larger meso-scale regions around the colony within avian foraging ranges (NE Newfoundland: Divs. 3Kh, 3Ki, 3La), and (3) the fishing regions of Labrador, Newfoundland and St. Pierre et Miquelon (Newfoundland: Divs. 2J, 3K to 3P) (Fig. 1). The spatial scales of these regions can be approximated as the distance between the headlands used to define each of the coastal fishing areas. Using this criterion, the spatial scale of the Funk Island Region is 140 km, NE Newfoundland is 310 km, and the Newfoundland region is 1400 km.

RESULTS

Seasonal variation in pelagic prey availability

Most of the major prey species that gannets feed to their chicks tend to prefer 'warmer' water and migrate into the Northwest Atlantic in late summer, when fisheries catches of these species are highest (Fig. 2). The seasonal pattern of catches varies among the 4 major pelagic species that are commercially exploited in the region. Short-finned squid and mackerel are summer migrants, and maximum catches are made during late

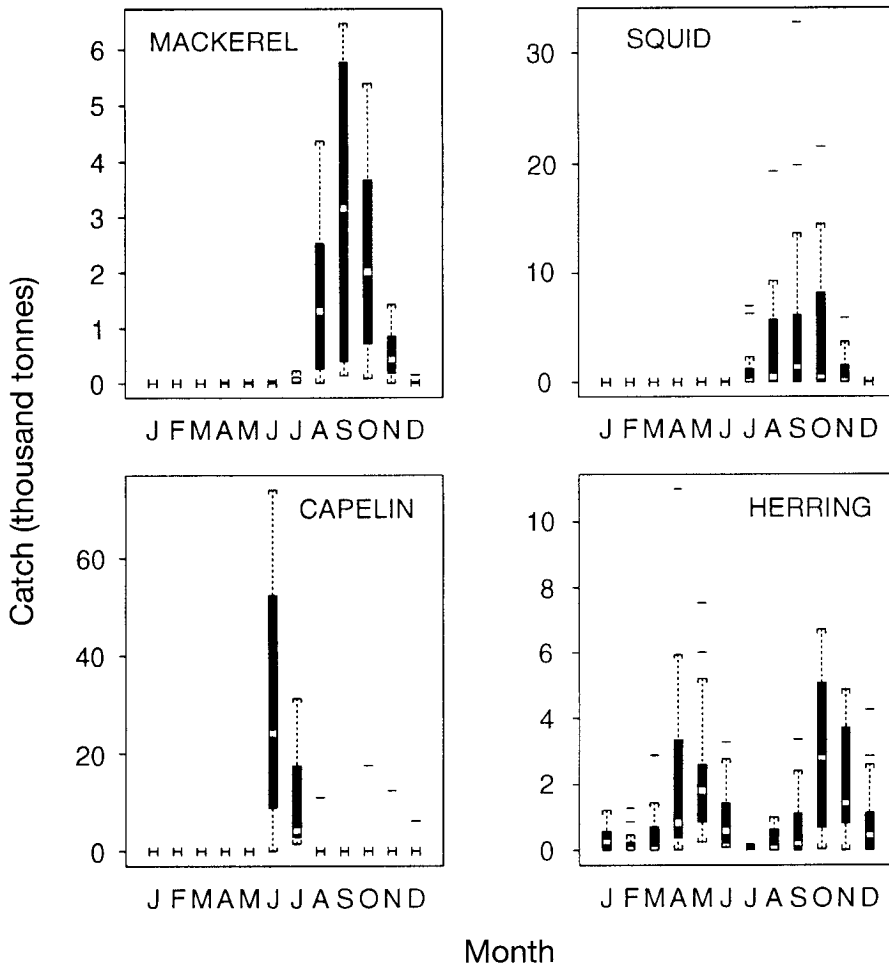


Fig. 2. Box plots of the seasonal patterns of fishery catches of mackerel *Scomber scombrus*, squid *Illex illecebrosus*, capelin *Mallotus villosus*, and herring *Clupea harengus* in the Newfoundland region, which show the ranges (within brackets), quantiles (black bars), medians (white portion of bars) and outliers (dashes, defined as points that are further away from the median than 1.5 times the inter-quartile range) for the monthly catches from 1977 to 1991

summer and early autumn when annual sea surface temperatures are highest. Another 'warm-water' species, Atlantic saury, also moves into the region in some years in late summer, but is not commercially exploited. Herring in the region usually occur inshore, and commercial exploitation is targeted mainly at spring spawning schools and at autumn feeding concentrations. Capelin is a cold water species, and inshore catches are made in early summer during the spawning migration from offshore regions. Large variation in the commercial catches of pelagic species is evident (Fig. 2); in some years there are very large catches, while in other years practically nothing is caught. Overall, the temporal patterns are relatively robust.

Relating gannet harvest to fishery-independent abundance estimates

The gannets' landings of squid were correlated with research vessel indices of abundance over a

wide oceanographic area (see Fig. 3). The correlations were high with the research vessel data off the Labrador coast (Div. 2J) and St. Pierre Bank (Div. 3PS), and the northeastern portion of the Scotian shelf (Divs. 4VN, 4VS; Table 2). The correlations with the Grand Bank region (Divs. 3K, 3L, 3N, 3O) were positive, relatively low and nonsignificant. The only negative correlation occurred on the central Scotian Shelf (Div. 4W). This analysis was repeated using Spearman's rank-order correlation in place of the Pearson product-moment correlation, and in all cases the correlations and significance levels were similar. The low correlations with the Grand Banks surveys may have resulted because the bulk of the squid caught are on the edge of the bank, and because catches depend greatly upon micro-scale variability in bottom temperature (Dawe & Warren 1992). The variability in the research survey data is many times that seen in the gannet data, and it is clear that gannet landings are not proportional to squid abundance estimates.

Scaling of associations between catches of mackerel and squid by seabirds and humans

Associations between the landings of squid and of mackerel by gannets at Funk Island and by inshore fisheries were broadly and highly correlated at the scale of large bays in the vicinity of Funk Island, both at the scale of more distant large bays and inshore regions around the Newfoundland coast and at the scale of the Newfoundland region as a whole (Figs. 3, 4 & 5).

Squid had a much wider range of association between seabird and fishery catches than did mackerel (Fig. 5). We could not reject the null hypothesis of no heterogeneity among the correlations for squid ($\chi^2 = 0.6$, $df = 11$, $p = 0.99$). There was, however, evidence that the correlations for mackerel are heterogeneous ($\chi^2 = 20.7$, $df = 12$, $p = 0.05$). The spatial scale for which the gannets' food samples provide information about commercial catch of mackerel is limited to eastern Newfoundland. For both mackerel and squid the strongest associations were found along Newfoundland's northeast coast in the general vicinity of Funk Island. Overall, avian and human harvests of mackerel and squid were highly correlated at local, meso and regional spatial scales in August vs August and in August vs annual comparisons (Figs. 6 & 7). The above analysis was repeated using Pearson product-moment correlation. The only difference was that the local correlations were higher for mackerel, though still smaller than the larger scale correlations.

These data series were autocorrelated. For example, for the gannets' harvest of squid, the lag-1 autocorrelation is 0.58, while for mackerel it is 0.43. This effectively reduces the number of degrees of freedom in the analysis. However, even when the number of degrees of freedom is reduced by the method of Bayley & Hammersley (1946), the results remain significant. A further check on the robust-

Table 2. Correlations of landings of squid by gannets *Sula bassana* on Funk Island with research vessel indices of abundance. NAFO divisions are given in Fig. 1 and also include the St. Pierre Bank (3PS), the northeastern portion of the Scotian Shelf (4VN, 4VS), the central Scotian Shelf (4W) and Brown's Bank on the southwestern portion of the Scotian Shelf (4X). n: years of data

NAFO division	r	p	n
2J	0.57	0.02	14
3K	0.33	0.27	13
3L	0.32	0.24	15
3N	0.24	0.24	14
3O	0.26	0.39	14
3PS	0.71	0.03	9
4VN	0.80	0.003	15
4VS	0.73	0.002	15
4W	-0.13	0.65	15
4X	0.36	0.18	15

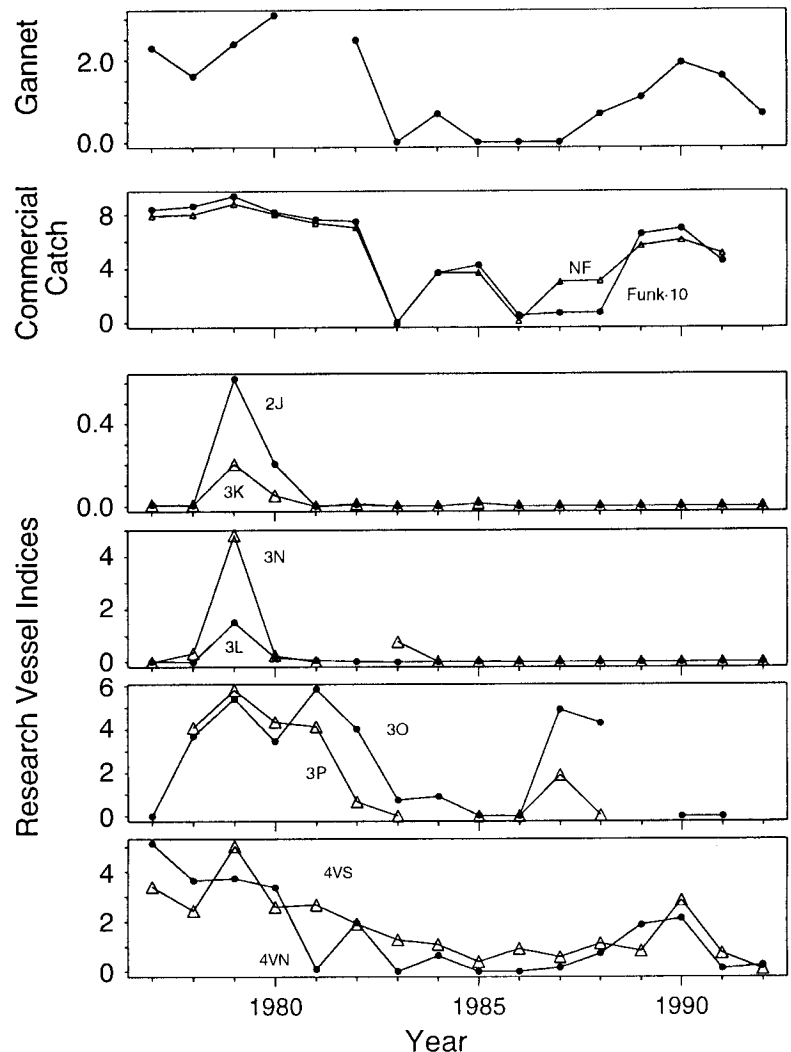


Fig. 3. Landings (% of total mass) of short-finned squid *Illex illecebrosus* by gannets *Sula bassana* on Funk Island, catches (t) by inshore fisheries in the Funk Island region (catch \times 10; 'Funk-10') and the Newfoundland region ('NF'), and research vessel indices in mean catch per tow for NAFO Divisions 2J, 3K, 3L, 3N, 3O, 3P, 4VS and 4VN. All data have been transformed by log (catch + 1)

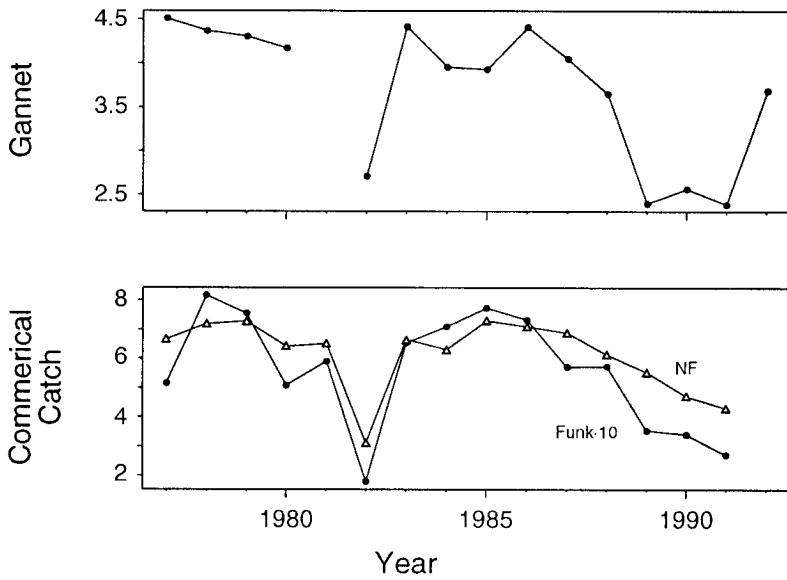
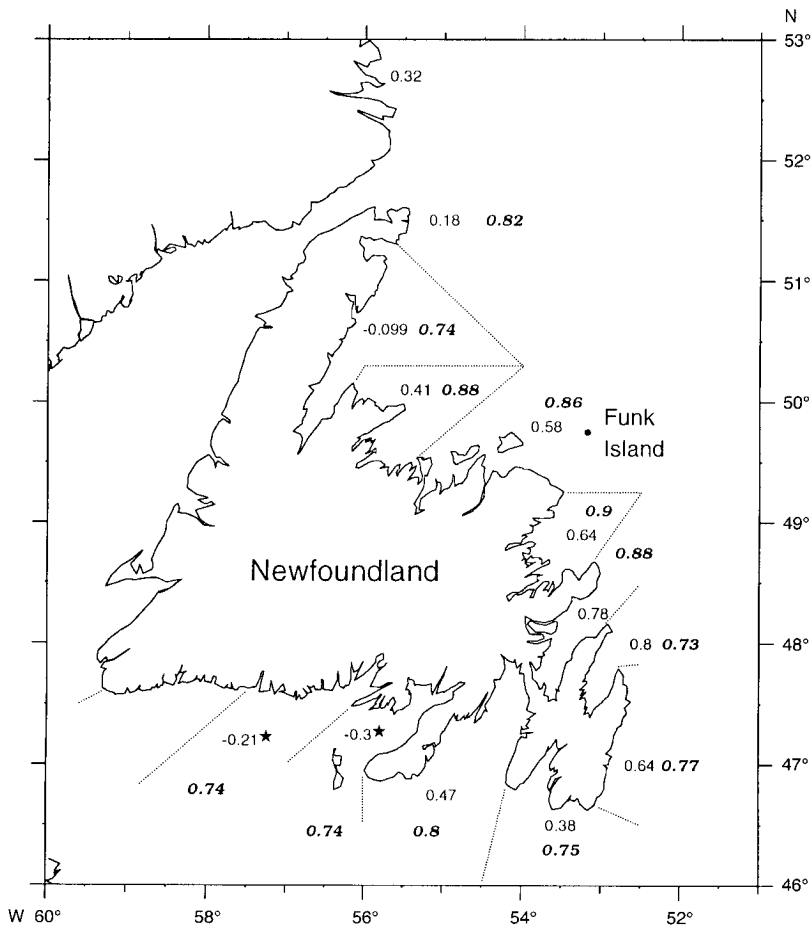


Fig. 4. Landings (% of total mass) of mackerel *Scomber scombrus* by gannets *Sula bassana* on Funk Island, catches (t) by inshore fisheries in the Funk Island region (catch $\times 10$; 'Funk-10') and for the Newfoundland region ('NF'). All data have been transformed by $\log(\text{catch} + 1)$



ness of the associations is to divide the annual time-series into 2, an early and late section, and repeat the analysis. The strength and significance of the correlations increased for almost all cases, demonstrating the strength of the relationships.

DISCUSSION

The prey landings of gannets at 1 breeding colony, sampled once each year over a 5 to 13 d sampling period in late summer, reflected fishery catches of the birds' major prey species on spatial scales up to 1000s of kilometres in extent. The seabirds' prey landings were associated with commercial fishery landings in August and with annual fishery landings; the seabirds' harvests of squid were also associated with fishery-independent indices of the abundance of squid over spatial scales of 1000s of kilometers. The robustness of these correlations is indeed striking. These findings support contentions that dietary data from seabirds are useful in predicting fishery conditions in local and meso-scale areas around breeding colonies (e.g. Montevicchi et al. 1987) and also in larger mega-scale regions beyond avian foraging ranges around colonies (e.g. Hislop & Harris 1985).

Why do we find strong correlations between the prey harvests of seabirds and of humans at spatial scales much larger than the gannets' foraging range and at monthly and

Fig. 5. Spearman rank-order correlations between the catches of squid *Illex illecebrosus* by gannets *Sula bassana* in August and the annual catches of squid by the fishery (bold italic type), and between the catches of mackerel *Scomber scombrus* by gannets in August and the annual catches of mackerel by the fishery (plain type), in Newfoundland bays and inshore fisheries regions. Correlations that are significantly different from the local correlation around Funk Island are marked with asterisks

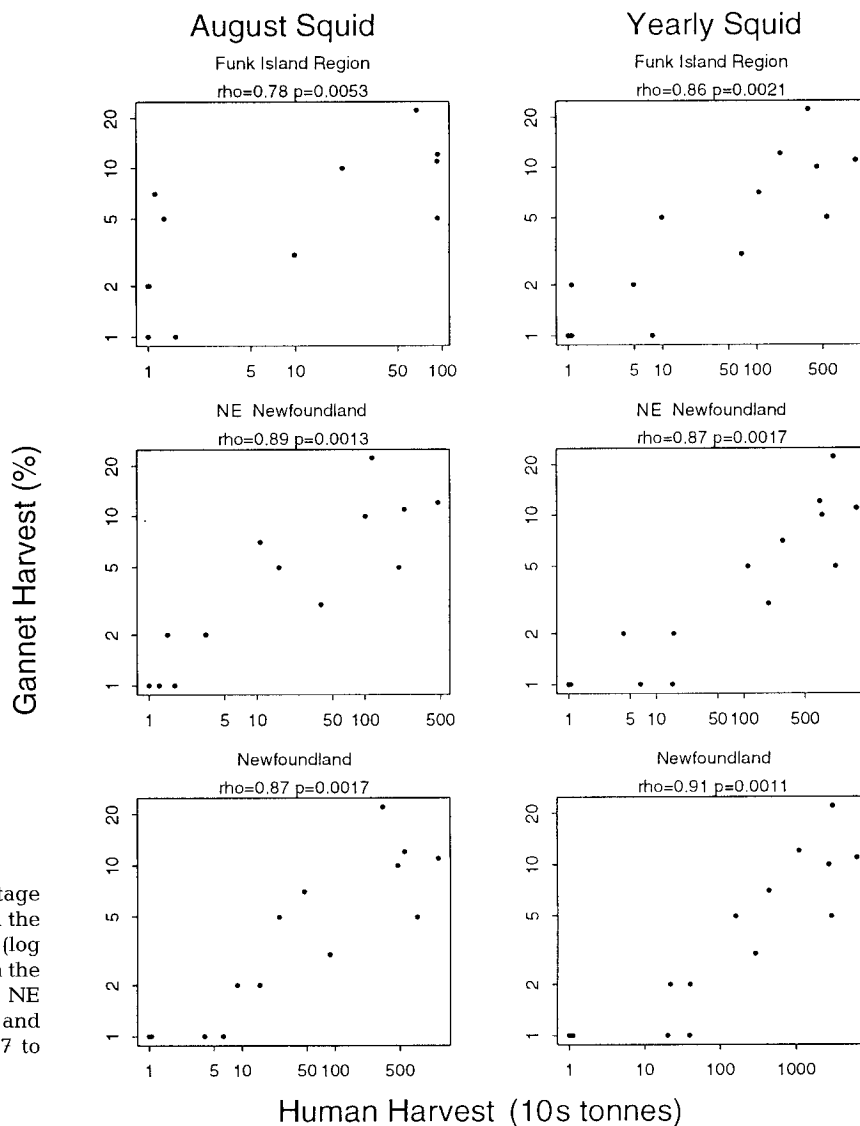


Fig. 6. Relationships between the percentage of short-finned squid *Illex illecebrosus* in the prey harvests of gannets *Sula bassana* (log scale) and commercial catch (log scale) in the Funk Island Region (NAFO Div. 3Ki), NE Newfoundland (Divs. 3Kh, 3Ki, 3La) and Newfoundland (Divs. 2J, 3K to 3P), 1977 to 1992

annual intervals that are longer than the seabird sampling period? These associations are not expected, because biotic and physical oceanographic interactions exhibit scale-dependent relationships (Hunt & Schneider 1987, Barry & Dayton 1991), and because pelagic food webs and the diets of conspecific seabirds often vary in different oceanographic regions (e.g. Schneider & Hunt 1984) and through time (Vermeer & Westrheim 1984, Duffy et al. 1987, Montevecchi & Myers 1992). Some explanation lies in the interaction of the biology of the prey and the spatial scale of environmental forcing. Atlantic mackerel and short-finned squid prefer water temperatures in the range of 9 to 12°C (Squires 1957, Hurley 1980b, Scott & Scott 1988), and the northward migration of these species was probably limited during summers with low catches of mackerel and of squid (Templeman & Fleming 1953,

Parsons 1970). Sea surface temperature varies on scales of 1000s of kilometers (Thompson et al. 1988), and the relationships over the space and time scales reported here may be caused by interactions of the thermal preferences of mackerel and squid with large-scale variations in sea surface temperatures. Variations in Gulf Stream strength (e.g. Drinkwater et al. 1994) may influence sea surface temperature which in turn may affect pelagic prey migrations into the Newfoundland region from more southerly regions. When waters are warm enough for migration into the Newfoundland region, mackerel and squid, if abundant, radiate over a very wide oceanographic area, such that sampling at a single point (seabird colony) in space and time provides a robust signal of a very broad-scale pattern. The biological significance of these relationships derives from interactions between mega-scale

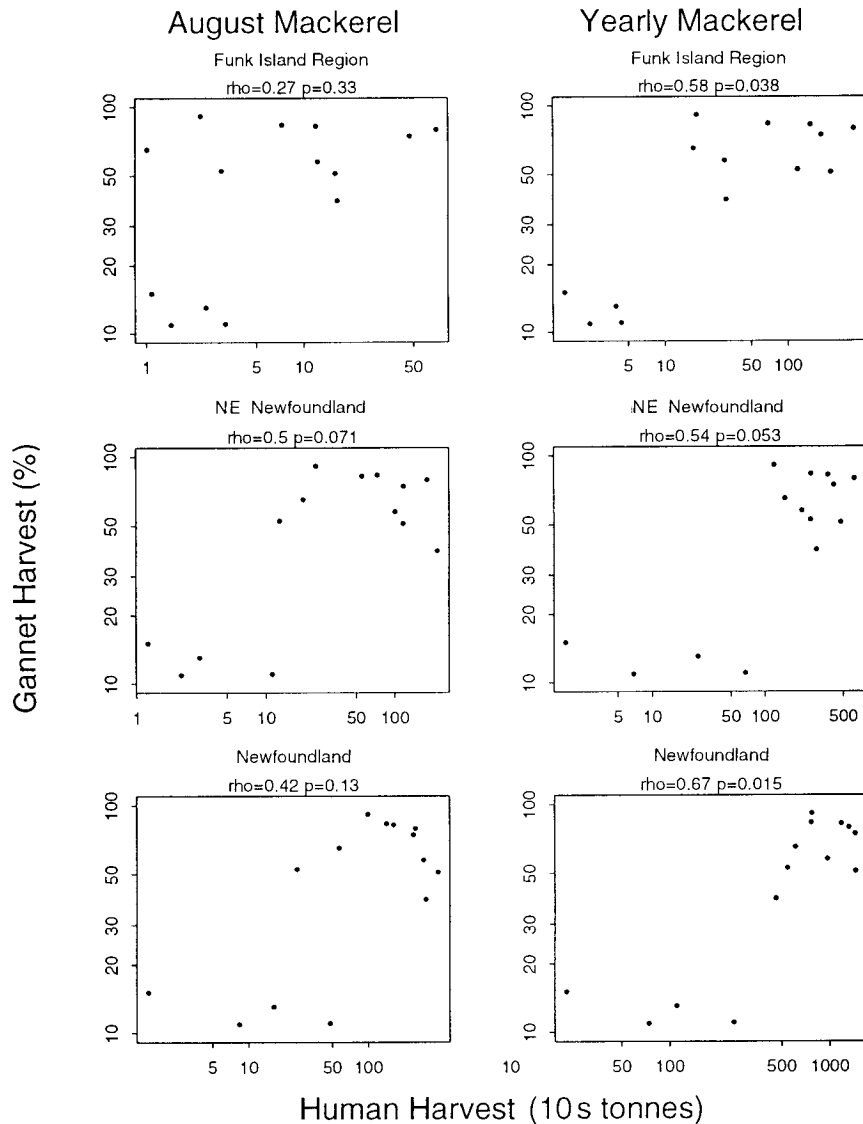


Fig. 7. Relationships between the percentage of mackerel *Scomber scombrus* in the prey harvests of gannets *Sula bassana* (log scale) and commercial catch (log scale) in the Funk Island Region (NAFO Div. 3Ki), NE Newfoundland (Divs. 3Kh, 3Ki, 3La) and Newfoundland (Divs. 2J, 3K to 3P), 1977 to 1992

physical events (surface water temperature) and biological responses (migratory movements) by pelagic squids and fishes. Similar relationships are predicted for many pelagic prey that migrate long distances into cold and high-latitude oceanographic regions (Coelho 1985). Large-scale biophysical associations and signals such as these (see also Aebischer et al. 1990, Bertram & Kaiser 1993, Mann 1993) will be informative to marine ecologists and oceanographers studying environmental change and the dynamics of marine food webs.

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