

SEABIRDS AS INDICATORS OF CHANGES IN MARINE ECOSYSTEMS: ECOLOGICAL MONITORING ON MACHIAS SEAL ISLAND

A. W. DIAMOND* and C. M. DEVLIN

Atlantic Cooperative Wildlife Ecology Research Network, and Biology Department, University of New Brunswick, P.O. Box 45111, Fredericton, N.B. Canada E3B 6E1.

(*author for correspondence, e-mail: diamond@unb.ca)

Abstract. Changes in marine ecosystems can be manifested in many different ways, on different temporal and spatial scales. Seabirds are top consumers in marine foodwebs and offer opportunities to detect and assess the biological effects of changes in physical parameters (sea-surface temperature [SST], salinity, depth of thermocline etc.) of the marine ecosystem. We compare six-eight years' of data on the biology (diet, and breeding success) of four species of seabird (arctic tern *Sterna paradisaea* and common tern *S. hirundo*, which feed at the sea surface; and Atlantic puffin *Fratercula arctica* and razorbill *Alca torda*, which dive 30–60 m for their prey) breeding on Machias Seal Island (MSI) in the Bay of Fundy with both our own meteorological and oceanographic measurements, and with standard measurements from conventional sources. These are compared with fisheries data on changes in the main prey of all the seabirds concerned (juvenile or '0-group' herring *Clupea harengus*) which are the most direct link between the seabirds and the physical properties of the marine system. We explore relationships between seabird productivity and diet, and other aspects of both herring biology (larval surveys, and fat content) and oceanography (SST data from the island, and remotely sensed data from the entrance to the Bay of Fundy). Timing of laying by puffins followed SST variation at neither the local (MSI) nor regional scales, but at the scale of the North Atlantic, following the trend of populations breeding off northern Norway. The proportion of herring in the diet of terns over 6 years varied inversely with herring larval abundance the previous fall; this relationship was not statistically significant in the puffin and razorbill. A major new finding is the considerable (~50%) inter-annual variation in the energy density (fat content) of juvenile herring that are the main seabird prey; breeding success of both species of tern varied in parallel with the energy density of juvenile herring in the diet until the last two years of the study, when sandlance (*Ammodytes* sp.) and euphausiid shrimp predominated in the diet. Our long-term research approach combines traditional population monitoring (of numbers of breeding birds) with demographic, behavioural and environmental monitoring, to provide new understanding of the marine ecosystem as well as of seabirds.

Keywords: Bay of Fundy, energy density, foodweb, Gulf of Maine, herring, indicators, Machias Seal Island, monitoring, puffin, razorbill, scale, sea-surface temperature, seabird, tern, weather

1. Introduction

Populations of seabirds, like those of other birds, are commonly monitored by those responsible for their conservation or management (Drury, 1973-74; Harris and Murray, 1981; Gaston *et al.*, 1988; Hatch *et al.*, 1994). Seabirds are also used



widely to monitor the occurrence and ecological impacts of pollutants such as oil and mercury in the marine environment (reviewed in Furness and Camphuysen, 1997); to detect changes in the availability of prey (e.g., Croxall *et al.*, 1988; Montevecchi, 1993; Barrett and Krasnov, 1996); and to reflect ecological impacts of oceanographic changes such as ENSO events (Schreiber and Schreiber, 1984). There is increasing interest in combining conventional monitoring of breeding population size with both demographic parameters (to provide some explanation of population changes) and relevant behaviours (such as foraging rate) that might both explain demographic changes and reflect changes in the marine ecosystem that are of interest to marine ecologists as well as seabird biologists (Bost and LeMaho, 1993; Furness and Greenwood, 1993).

Seabirds are long-lived organisms that spend most of their lives at sea but nest on islands in colonies, usually of several species. Because they nest on land, most knowledge of seabird biology has been obtained during that relatively short part of their annual cycle. Even when nesting, they have to return to the sea to find food for themselves and their young. This acts as a major constraint on their life history and makes them dependent on oceanographic conditions throughout their lives. As a group, seabirds are predators near the top of marine food-webs; the species we are concerned with here feed on small schooling fishes and planktonic invertebrates, especially crustacea. Seabird breeding success is obviously vulnerable to changes in abundance of their prey species around the colonies (Cairns, 1987; Montevecchi *et al.*, 1988; Monaghan *et al.*, 1989; Bost and LeMaho, 1993). Conversely, seabirds may consume as much as 20% of the secondary productivity of waters around colonies (e.g. Furness, 1978), and because seabirds are often highly size-selective in their feeding they are theoretically capable of affecting the population dynamics and hence the long-term abundance of their prey (Cairns, 1992). Those seabirds that feed on commercially harvested species can also reflect changes in stock size, for example by population changes in parallel with changes in stock abundance (e.g., Montevecchi and Berutti, 1990). Seabird breeding biology may indicate short- and long-term changes in oceanographic conditions over much larger areas than the immediate foraging grounds around the colony (Schreiber and Schreiber, 1984; Hunt and Schneider, 1987; Croxall *et al.*, 1988; Kitaysky and Golubova, 2000). One long-term study in the North Sea has shown that population size, breeding success and survival of black-legged kittiwakes (*Rissa tridactyla*) integrate changes in the marine ecosystem from sea-surface temperature through plankton and fish, over decadal time-scales (Aebischer *et al.*, 1990).

Seabirds respond to changes in their marine environment over a variety of temporal and spatial scales. While nesting, they make hour-to-hour decisions on where to feed, and which prey to search for, and need to balance activities over hundreds of square kilometres at sea (mainly feeding in most species, but including courtship and other social activities in others) with those on land. Terrestrial activities, often confined to areas of less than a hectare, are concerned with finding and keeping a mate and a nesting site, and protecting eggs and young against predators and

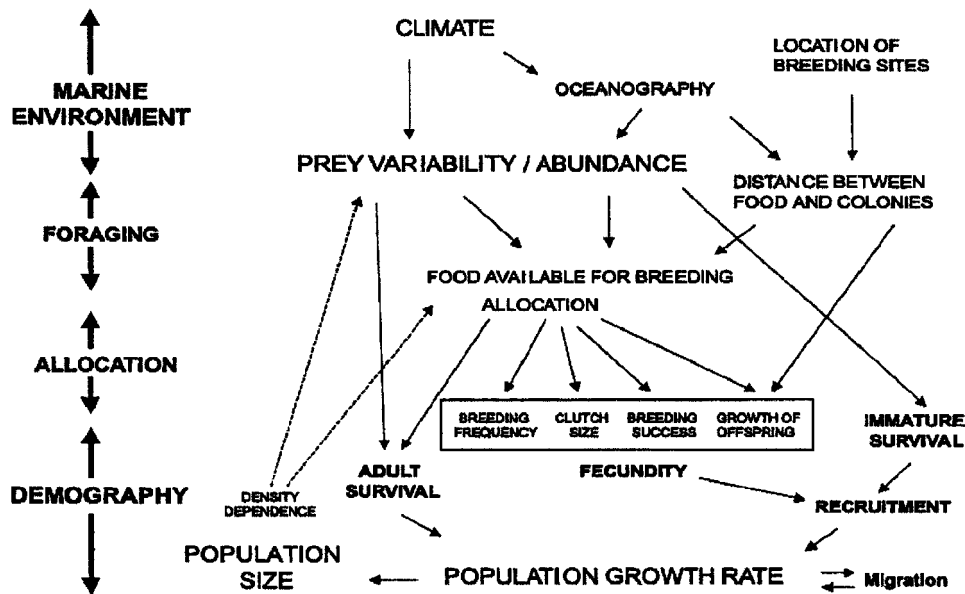


Figure 1. General relationship among weather and oceanographic variables, and seabirds (from Weimerskirch, 2001).

extreme weather. Over the course of the 3–4 months of the local breeding season, their offspring hatch and grow (requiring different food), the weather (usually) ameliorates, and prey may change in location and availability; the breeding success at the end of the season integrates the results of the decisions made by the birds in response to these changing demands and opportunities. Like other long-lived species (mean adult life spans of over 20 years are not uncommon in seabirds), there are life-history trade-offs to be made between investing in future generations (reproduction) and in ensuring their ability to breed again in future years (survival) (Johnsen *et al.*, 1994). A tern or puffin nesting on a small offshore island may forage within a few kilometres of the island throughout the breeding season, but then migrate through coastal or pelagic waters to very different winter habitats thousands of kilometres distant. The fitness of an individual seabird must integrate these complex and multi-scale responses to its marine environment.

Such complex influences contrast sharply with those of more sessile organisms commonly used as bio-indicators. The mobility and longevity of birds are sometimes regarded as reducing their utility as bio-indicators, but those same attributes also equip seabirds with the potential to indicate environmental changes over scales, and in systems, that are otherwise very difficult of access (Burger and Gochfeld, 2001). The challenge is to understand the responses of the birds to environmental change over all spatial and temporal scales in sufficient detail to allow us to use them in that way (Bost and LeMaho, 1993).

TABLE I
 Framework for responses of seabirds to broad categories of environmental change. Note that the same response can be affected by different changes in the environment

Environmental change	Seabird response	Time scale	Spatial scale
Prey availability	Foraging effort	short (hours/days)	small (foraging range)
Prey availability	timing of breeding	medium (days/weeks)	small (foraging range)
Prey availability	Breeding success	medium (weeks/months)	small (foraging range)
Prey availability	adult survival	long (years, decades)	large (entire migratory range)
Extreme weather	foraging effort	short (hours/days)	small (foraging range)
Extreme weather	breeding success	medium (weeks/months)	small (foraging range)
Extreme weather	adult survival	long (years, decades)	large (entire migratory range)
Climatic/oceanographic change	Distribution (range)	years	large
Climatic/oceanographic change	timing of breeding	days/weeks	large
Climatic/oceanographic change	breeding success	weeks/months	large
Climatic/oceanographic change	adult survival	years/decades	large

The appropriate theoretical framework for the part of this task that relates seabirds to the availability of their prey was set by Cairns (1987). The broader framework relating seabird demography to their marine environment is outlined in Figure 1 following Weimerskirch (2001). In Table I we summarize seabird responses to both weather and oceanographic conditions, and identify the temporal and spatial scales to which they refer. The categories used are very broad, and are illustrative rather than definitive; for example, 'breeding success' integrates the decision whether or not to breed, the size and number of eggs laid, the number and condition of chicks hatched, and their growth rates. Each of these components of breeding success can be measured separately in order to more precisely assess the environmental factor responsible for any change in breeding success.

Our research on Machias Seal Island is directed towards measuring and understanding these responses through intensive long-term study of the diet and demographics of a community of four species (arctic and common terns *Sterna paradisaea* and *S. hirundo*, Atlantic puffin *Fratercula arctica*, razorbill *Alca torda*) exploiting different parts of the oceanic food-web. Our study site is a relatively accessible colony situated at the ecotone between the cold Bay of Fundy and the warmer Gulf of Maine, where changes in the oceanic system are likely to be manifest sooner than at sites situated more centrally in marine ecozones. Three of the four species of seabird (puffin, razorbill, arctic tern) are at or close to the southern edge of their breeding range, whereas common terns extend for thousands of kilometers south and north; the site is therefore well placed to detect large-scale climatic or oceanographic changes that would be expected to affect these species differently. First, to determine the appropriate spatial scale at which to assess the birds' responses to changes in their physical environment we examine whether the meteorological and oceanographic data we collect are representative of a larger area (such as the foraging area around the colony), or are specific to the immediate vicinity of the colony. Second, we compare eight years of data on seabird biology (diet and breeding success) with both our own meteorological and oceanographic measurements, and with standard measurements from generally available sources. Third, we explore relationships between diet and breeding success of the seabirds with changes in their main prey species (juvenile herring *Clupea harengus*), which provide a direct link between the seabirds and the physical properties of the marine system. The results we present are preliminary, from a long-term 'work in progress', rather than definitive; our conclusions are subject to revision as longer time-series accumulate.

Our research is constrained by the lack of independent data on the abundance or availability of juvenile herring in this area; herring stocks are not sampled between the larval stage and their recruitment into the fishery two years later. Previous work by our research group (Amey, 1998) showed a strong relationship between the % herring in the diet of arctic terns (*Sterna paradisaea*) and the catch-per-unit-effort (CPUE) of herring in the weir fishery of Grand Manan, 20–30 km away, two years later. Here we explore other aspects of the relationships between seabird diet and

herring (larval surveys and fat content), and climatic and oceanographic data (our own from Machias Seal Island, and conventional and remotely-sensed data from other sources). We now have enough data from the 4 species of seabird to make inter-specific comparisons in an attempt to address the question ‘which seabird **best** reflects/predicts significant changes in the system?’

1.1. RELATIONSHIPS AMONG OCEANOGRAPHY, WEATHER, AND SEABIRDS

The general relationship among weather and oceanographic variables, and seabird biology, is illustrated in Figure 1 (Weimerskirch, 2001). The oceanographic parameter most commonly associated with seabird biology is sea surface temperature (SST), for two reasons: it reflects broad physical characteristics of the water body; and it directly affects the distribution and abundance of prey species, many of which are sensitive to changes of only a few degrees in SST. It has the advantage over some other variables (e.g. salinity) of being easily measured in the field with simple equipment, and of also being measured over large spatial scales from satellites which transmit digital data which are widely available on the Internet (Department of Fisheries and Oceans, 2001). SST may affect seabirds both directly (for example, the species found in waters of arctic origin are different from those found in tropical waters), and indirectly through effects on the species, abundance or availability of prey. Weather (i.e., atmospheric variables such as air temperature, precipitation, wind speed etc.) affects adult seabirds to some extent, particularly in their ability to catch prey (Dunn, 1973) but is particularly important to their young (chicks) during the few weeks of summer when they grow and develop. Most (~80%) of the energy in the food brought to seabird chicks by adults does not become seabird tissue but is used in maintenance (including thermoregulation) (Klaassen, 1994), so the amount of food diverted to keeping the young warm and dry will obviously affect their chance of survival. Weather during the chick-growth period will thus affect the growth rate and fledging conditions of chicks, independently of effects of availability and quality of prey in the diet (Dunn, 1975; Paquet, 2000).

1.2. STUDY SITE AND METHODS

Machias Seal Island (hereafter MSI) is a small (9.5 ha.) treeless island 19 km south of Grand Manan Island and 10 km off the coast of Maine, at the junction between the cold waters of the Bay of Fundy and the warmer Gulf of Maine to the south (Figure 2). The bedrock is granitic, with basaltic intrusions. On the south and west coasts there are wide expanses of bare rock with large storm-driven boulders forming a berm between the bare rock and the vegetated interior; on the more sheltered northern and eastern shores the boulders are much smaller and smoother, with a cobble beach between the boulders and the bare rock zone. The interior of the island is vegetated with a variety of grasses and sedges, with taller vegetation such as New York aster (*Aster novi-belgii*) and yarrow *Achillea lanulosa* (Hinds,

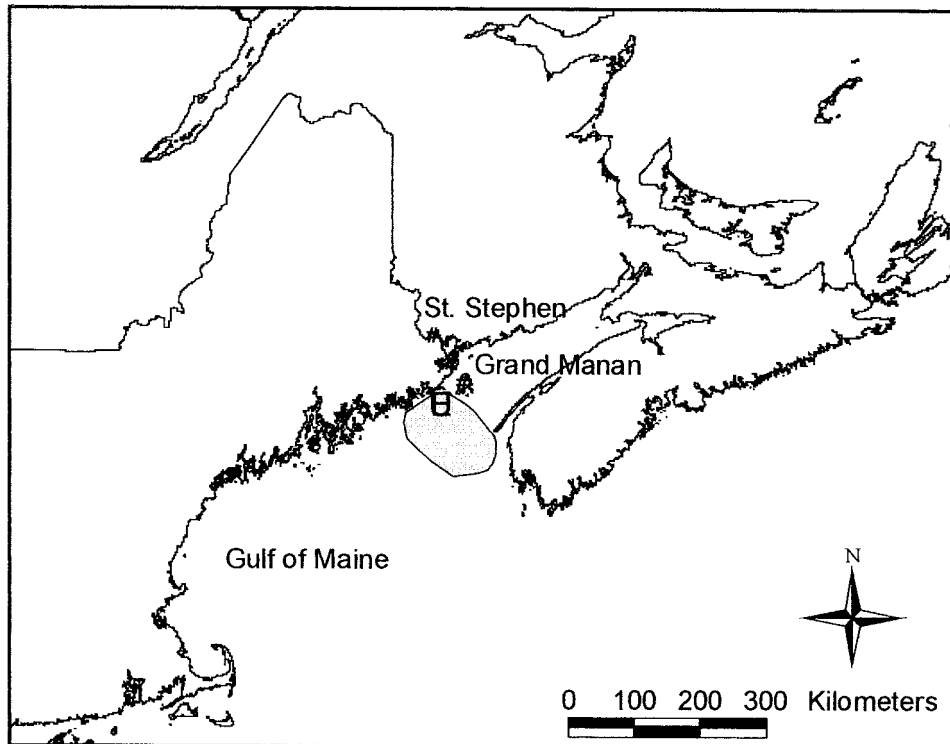


Figure 2. Map of Bay of Fundy and Gulf of Maine showing location of Machias Seal Island (starred) and area covered by Block 53 of the Department of Fisheries and Oceans SST database (see text) (shaded). From www.ngdc.noaa.gov/mgg/shorelines/shorelines.html.

1997). The terns nest mainly around the edge of the vegetated area, with lower densities in the interior and the upper part of the bare rock zone. Razorbills nest mainly under boulders, concentrated in the south-west and western boulder zones. Puffins nest in here too but also in earth burrows at the edge of the boulder berm and among the smaller boulders along the north-east shore. A systematic study grid is staked every 30 m at the junctions of grid lines aligned (magnetic) N-S and E-W.

MSI is a Migratory Bird Sanctuary owned by the Canadian Coastguard and managed by the Canadian Wildlife Service of Environment Canada. The seabird colony is protected by regulating the impact of tourists landing to view the seabirds, and by preventing nesting by herring gulls (*Larus argentatus*) and great black-backed gulls (*L. marinus*) which formerly reduced breeding success of the other seabirds by eating their eggs and young. There are no other predators on the colony, so we can assume that the seabird responses we measure are much less complicated by the effects of predation, and interactions between predators and observers, than they are on most seabird colonies where gulls also breed. We therefore expect to be able to detect seabird responses to oceanographic changes more clearly here than might be possible on colonies with more predators.

The four species of seabird studied intensively are all migrants: arctic terns undertake the longest annual migration of any bird, wintering in the Antarctic (Hatch, in press); common terns winter in eastern South America, as far south as Argentina (Nisbet, 2002); Atlantic puffins probably winter in the open North Atlantic, though their wintering areas are not clearly known (Lowther *et al.*, in press); and razorbills winter mainly in the Gulf of Maine (George's Bank) and outer Bay of Fundy (Chapdelaine *et al.*, 2001). Puffins begin laying in early May, razorbills about 3 weeks later; the terns arrive in numbers at the end of May and lay synchronously, peaking usually in the first week of June. Terns nest on the ground and are counted systematically every two years; numbers between 1994 and 2002 have varied between 370 and 1349 pairs of common tern and from 1640 to 2348 pairs of arctic tern (Diamond, 1999; Devlin and Diamond, 2002). Puffins and razorbills nest underground or beneath boulders and so are much harder to count; the first systematic censuses estimated 2,800 pairs of puffin in 1999 (Diamond and Robinson, unpublished MS) and about 530 pairs of razorbill in 2000 (Grecian and Diamond, unpublished MS).

For each seabird species we determine the breeding phenology (first and mean dates of egg-laying), clutch size (number of eggs laid per nest), and breeding success (separated into hatching and fledging) (Table II); research protocols are described in Devlin and Diamond (2001), and Diamond *et al.* (2002). Diet and foraging effort are determined in scheduled intensive watches from observation blinds during which we record the species, number and length (relative to the adult's bill) of prey brought to the chicks in a small number of marked nests visible simultaneously from the blind. Annual survival is estimated through systematic recapture and resighting of individually banded birds, using Capture-Mark-Recapture analysis (Clobert and Lebreton, 1991). Systematic weather measurements allow us to separate effects of weather, climate and oceanographic changes from those of prey availability (Table I). Rainfall is measured daily using a standard Environment Canada rain-gauge, air temperature is recorded by a digital thermometer with the probe in the shade of the house, visibility (and fog) by reference to local landmarks, wind speed and direction using a tower-mounted anemometer, and sea-surface temperature using a bucket dropped into the sea off the rocks; the latter measurement is made daily at 12 noon, other measurements twice-daily at 09:00 and 21:00 ADST. Variables measured twice daily are presented here as the mean of those two readings. Where possible we include all 8 years of data available to us, and explore relationships using standard statistical approaches including an α level of .05 for significance; with only 8 years of data the power to detect relationships is generally low so we look for patterns in the data using graphical presentations where appropriate.

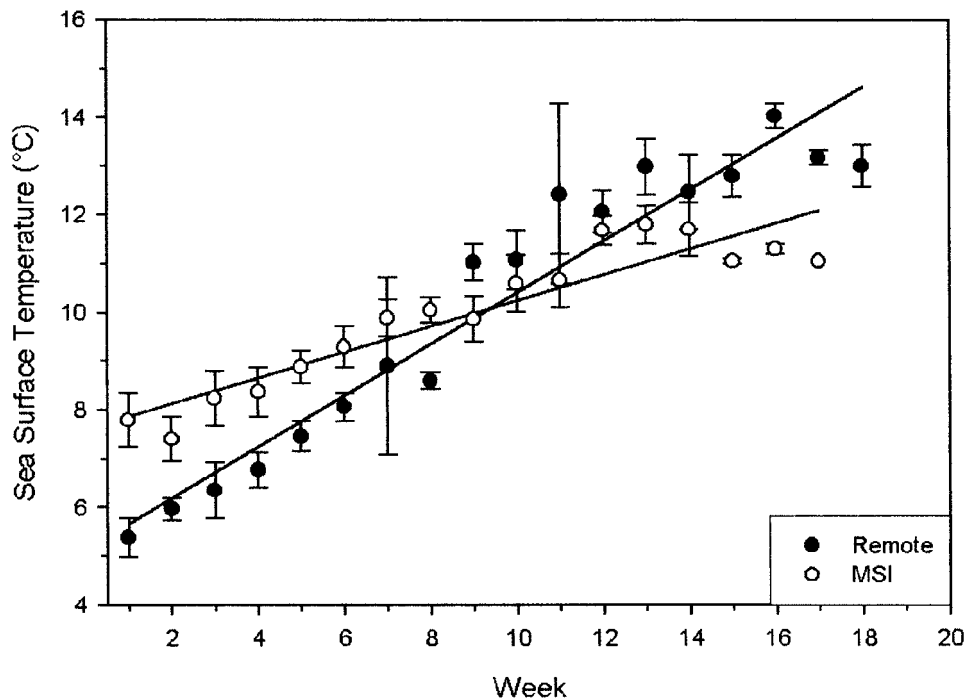


Figure 3. Relationship between sea-surface temperature (SST) measurements from Block 53 (Gulf of Maine/Bay of Fundy nearest to Machias Seal Island) ('remote') and Machias Seal Island for 1995-2000 combined, May through August. Week 1 = first week of May. Correlations between monthly means ($\pm 95\%$ confidence intervals) in the two data sets were statistically significant in all years; R^2 values ranged from 0.641 in 1995 to 0.924 in 2000.

2. Representivity of Local Weather Data

Weather data collected on the island may not be representative of the weather conditions faced by the seabirds as they roam the region in search of food. Feeding ranges have not been measured locally but the literature suggests that these species may travel at most 30–50 km from the colony in search of food (though most food is probably caught much closer than this – feeding flocks are regularly seen within a few hundred metres of the island). We therefore assess the extent to which our own local data, collected on the island, reflect conditions over a wider area. For sea surface temperature we compare MSI data with measurements from Block No. 53 on the DFO website (DFO, 2001). This comparison extends only through year 2000; data for 2001 and 2002 were not available to us. For weather variables we compare MSI data with the Canadian weather station nearest to MSI, at St. Stephen, N.B. (90 km north of MSI), from 1995 through 2002; these data are daily means of measurements taken at varying frequencies but always more often than those on MSI.

TABLE II

Seabird parameters monitored annually on Machias Seal Island (Diamond, Devlin and Amey, 2002)

Parameter	Method
Breeding Phenology and success	
Laying date	Systematic check of sample of nests; daily (terns), periodic (~10-d) auks
Egg size	Weigh and measure sample of fresh eggs (terns, razorbills) ¹
Clutch size	Maximum number of eggs recorded in sample nests (terns; clutch size constant in auks)
Hatch success	Number of chicks hatched per egg laid
Chick growth rate	Rate of increase in mass and wing length of sample chicks measured during linear phase of growth
Fledge success	Number of chicks fledged per chick hatched, i.e. flying (terns) or permanently leaving nest (auks)
Productivity	Number of chicks fledged per egg laid
Adult condition	
Body mass/size	Body mass divided by wing length (i.e. corrected for body size); currently measured systematically only in arctic terns
Annual survival	Rate of return of individually-marked (banded) adults, detected by both resighting and recapture; estimated using Capture-Mark-Recapture models
Feeding ecology	
Diet	Species and length (by reference to bird's bill-length) of prey items brought to chick, in systematic observations from permanent blinds
Foraging rate	Rate of delivery of prey items to marked nests (currently available for terns only)
Food quality	% fat in collected specimens of major prey category (herring)

¹Puffin eggs are not weighed because puffins are extremely prone to abandon eggs if disturbed during laying and early incubation.

2.1. SEA SURFACE TEMPERATURE

Correlations between daily SST measurements from Block 53 and MSI were statistically significant in all years; R^2 values ranged from 0.64 in 1995 to 0.92 in 2000 (Figure 3). Both slope and intercept varied among years so we cannot say that the local measurements bear a consistent relationship to the regional; on average MSI temperatures were about 2 °C above the regional in May but increased more slowly during the summer so were ~ 2 °C cooler by the end of July and early August (Figure 3).

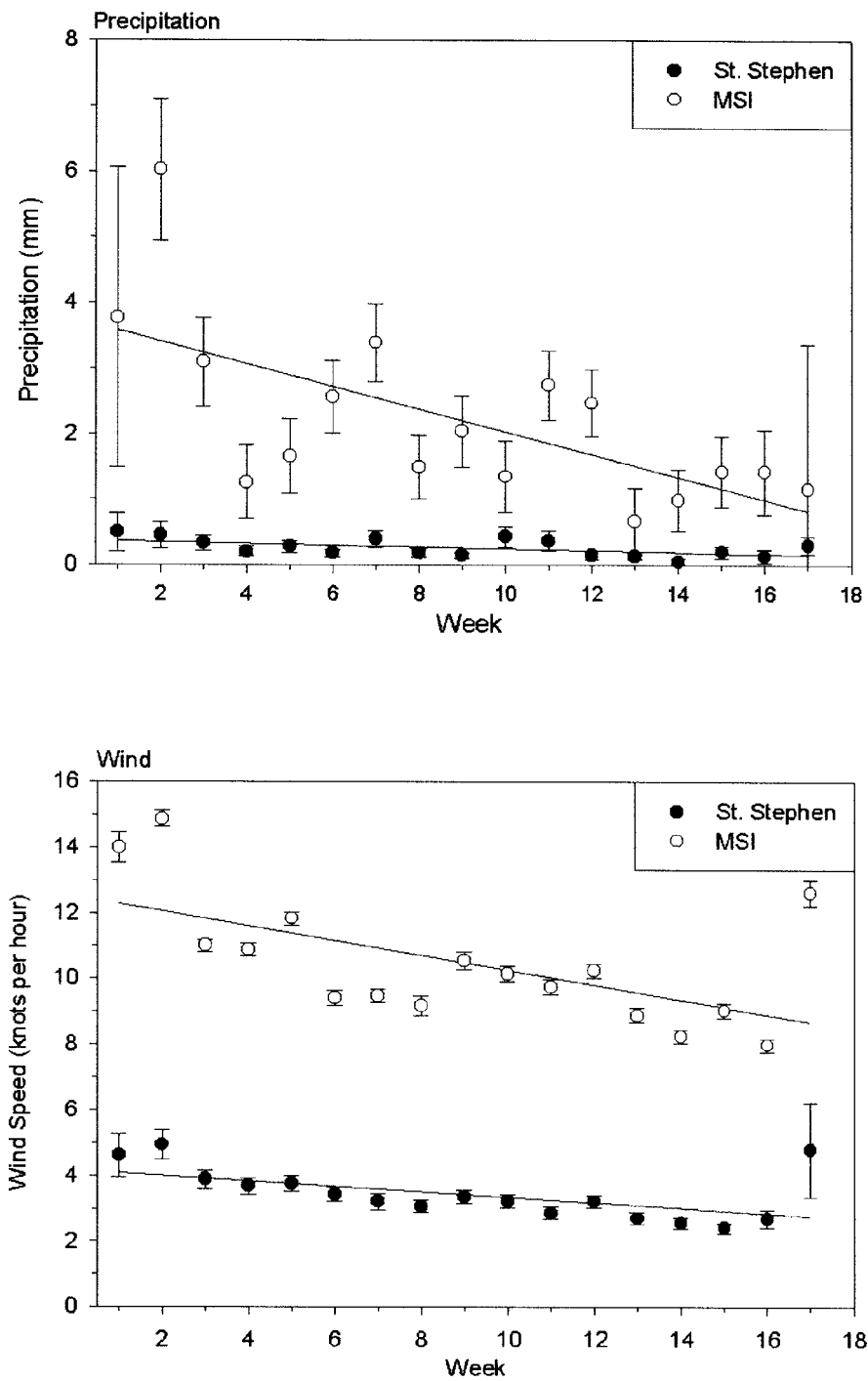


Figure 4. Comparison between monthly means (\pm S.E.) of precipitation and wind speed recorded at St. Stephen, N.B., and Machias Seal Island, 1995–2002 combined, May through August. Lines indicate calculated regressions.

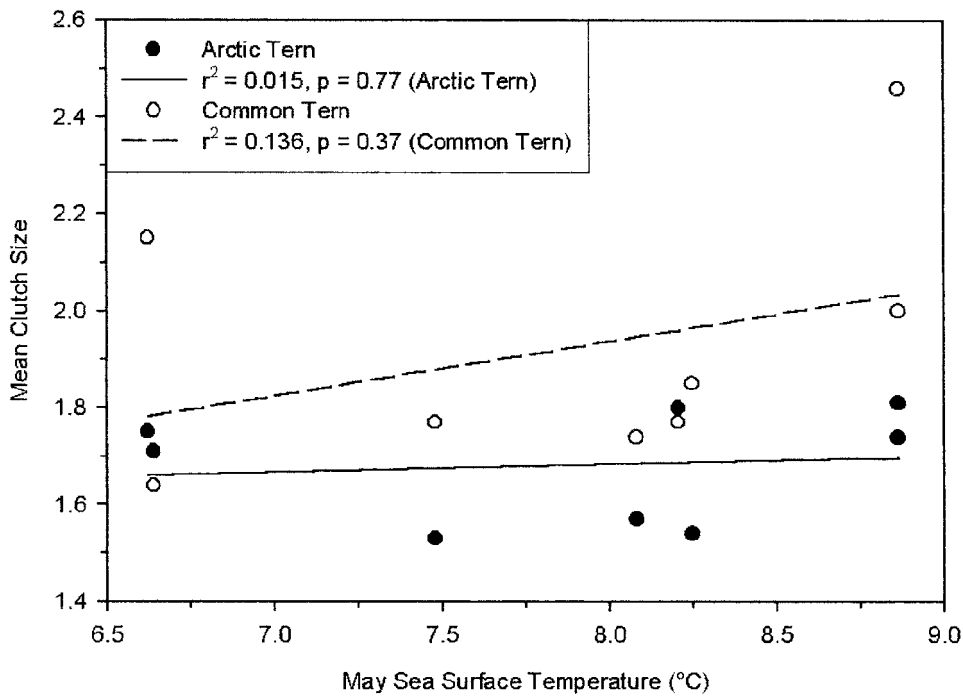


Figure 5. Relationship between clutch size of arctic and common terns, and May SST measured locally.

2.2. AIR TEMPERATURE, WIND SPEED AND PRECIPITATION

Comparisons between MSI data and those from St. Stephen (National Climate Data Center, 2001) showed little correlation (Figure 4). Mean and maximum air temperatures were lower on MSI than at St. Stephen, but minimum air temperature was higher, so there was consistently a smaller temperature range on the island than on the mainland. Precipitation was generally higher on MSI, and the island had consistently higher wind speeds. These differences are expected when comparing an oceanic site (MSI) with one on the mainland; the oceanic site has a cooler, windier, and more equable climate.

3. Seabird Responses

3.1. CLUTCH SIZE

SST is likely to affect clutch size (the number of eggs laid per nest) only in May, when the terns are developing their eggs (puffins and razorbills have an invariant clutch size of one). Accordingly we looked for a relationship between May SST and clutch size in common and arctic terns, but none was statistically significant (Figure 5).

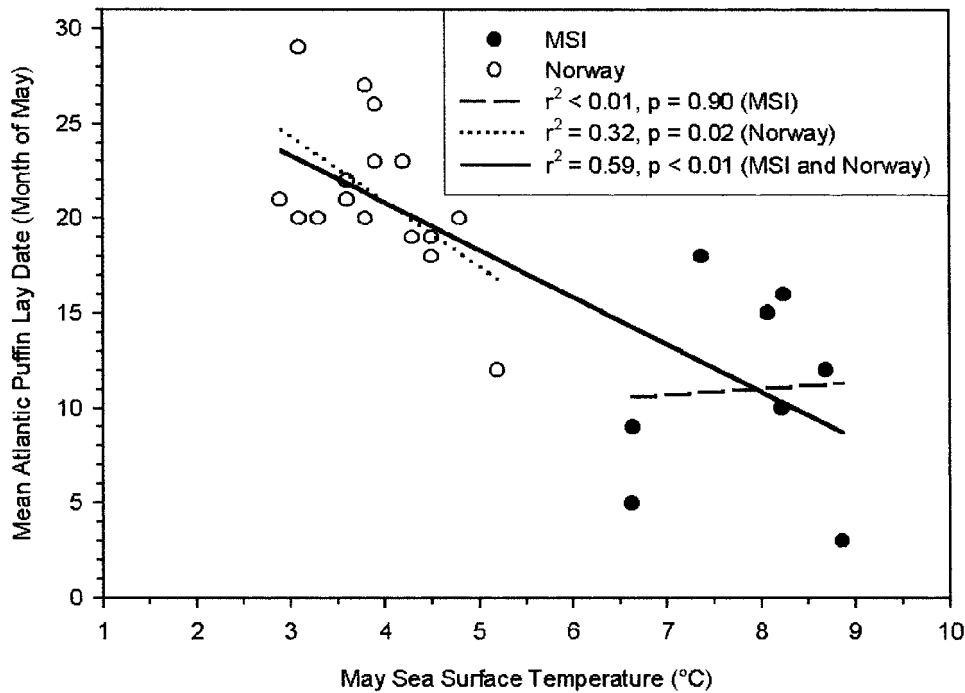


Figure 6. Relationship between mean laying date of puffins and mean sea-surface temperature (SST) in May, 1995–2002. Norwegian data from Barrett (2001). MSI data alone show no significant trend, but the regression line including MSI and Norwegian data combined explains more variation (higher r^2) than that through Norwegian data alone.

3.2. LAYING DATE

In some species, e.g. puffins, egg-laying date is correlated with sea-surface temperature; puffins are cold-water species and their laying date in Norway is negatively correlated with sea-surface temperature (they lay earlier in warmer springs) (Barrett, 2001). The relationship between puffin laying date and sea-surface temperature in May is shown in Figure 6; laying date shows no relationship with local SST, but the regression line through the Norwegian data is very similar to that through the Norwegian and MSI data combined, showing that the response of MSI puffins to SST is consistent with that of puffins in Norway.

3.3. PRODUCTIVITY (BREEDING SUCCESS)

The weather most likely to affect productivity is that during the early growth period of chicks, before their plumage is developed enough to keep them warm and dry. This two-week ‘critical’ period was calculated for each species in each year; we found little relationship between productivity and any weather variable over these periods (Figure 7). The only statistically significant relationship (negative, with precipitation, in razorbills) was driven by low productivity in one year of unusually

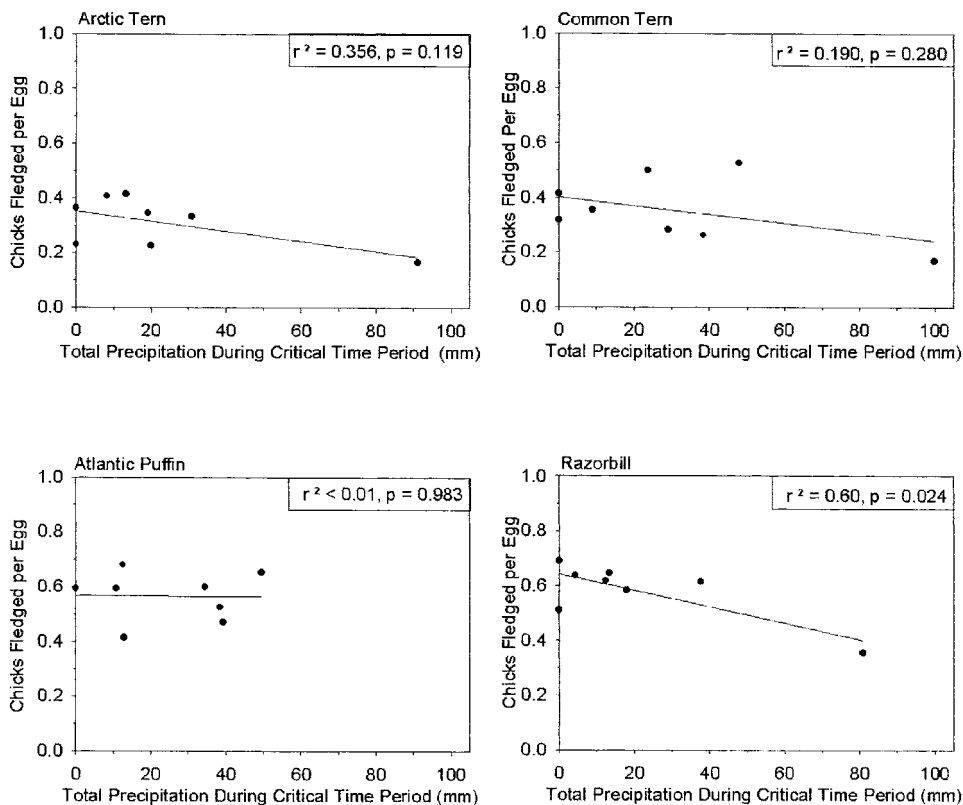


Figure 7. Relationships between precipitation during the most sensitive period of chick growth (see text) and breeding success in seabirds on Machias Seal Island, 1995–2002.

high precipitation (1998), and is suspect because we believe razorbill productivity was under-estimated in that year. Accordingly we conclude that, at least at the scale of comparisons among years, temperature, rainfall and windspeed have not significantly affected productivity in any of the four species during our study.

3.4. DIET

Atlantic herring was the prey species taken most frequently by all species in the early years of the study (Figure 8), except in 1998 when puffins took mostly white hake (*Urophycis tenuis*), silver hake (*Merluccius bilinearis*) or fourbeard rockling (*Enchelyopus cimbrius*); these species are impossible to distinguish in the field, at least in the size ranges taken by the seabirds, and are recorded in the field as ‘hake’. In the last two years herring has declined in the diets of all four species, replaced in 2001 by sandlance and in 2002, in the first part of the season, by euphausiid shrimp (krill). Even when herring predominated generally, the extent to which it dominated the diet varied considerably between species, and between years in most species; the exception is razorbill which took >60% herring in all years but one (Figure 8).

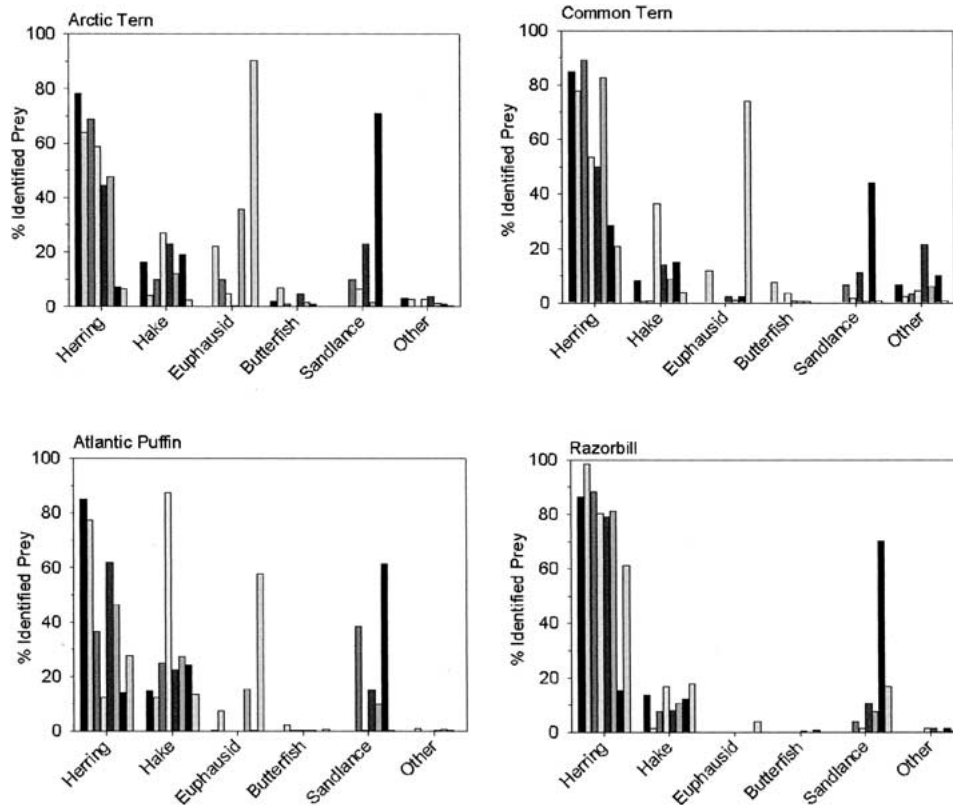


Figure 8. Annual variation in the diet of seabirds at Machias Seal Island. Bars show years, 1995-2002 from left to right. Data are % by number of each prey category.

The percent herring (by number of items) was particularly variable between years in puffin and arctic tern (Coefficient of Variation 61% puffin, 57.6% arctic tern, 43.8% common tern and 35% razorbill). In arctic terns, the percent herring in the diet predicted the Catch-per-Unit-Effort (CPUE) of herring in the Grand Manan weir fishery two years later (Amey, 1998). This is consistent with the fact that the seabirds eat '0-group' herring (those hatched the previous fall) while recruitment of herring to the weir fishery occurs at two years of age. Since herring is probably the most energy-rich item in the diet of these seabirds, we would expect seabird productivity to be higher in years of high percent herring in the diet, but we found no significant relationship in any species between productivity and percent herring in the diet (Figure 9) (see Energy Density, below).

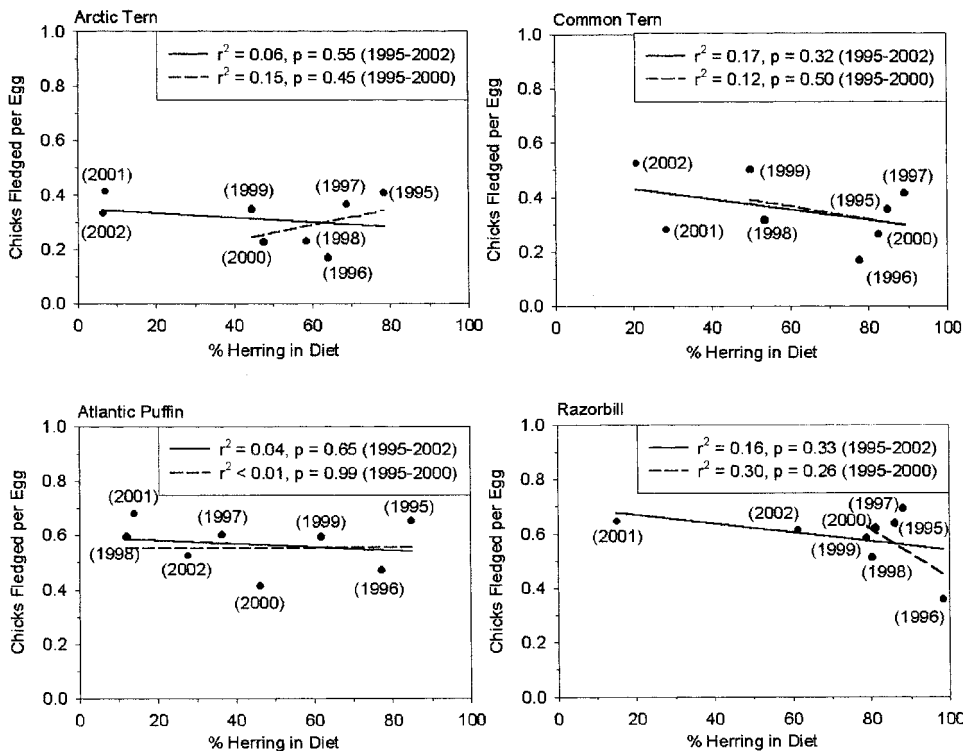


Figure 9. Relationship between percent herring in diet and productivity of seabirds on Machias Seal Island, 1995–2002.

4. Herring Characteristics

4.1. ENERGY DENSITY

An aspect of seabird diet not previously addressed by seabird biologists is the year-to-year variation in energy density (i.e., kCal per g) of the fish; it is normally treated as a constant. We collected herring dropped by seabirds on Machias Seal Island, and measured energy density directly in 1995 and 1996; in those years we found a significant inverse relationship between energy density (i.e., fat content) and water content. In subsequent years, following these results and the more general finding of Iles and Wood (1965) that the relationship is close enough to justify using % water to estimate % fat, we estimated energy density indirectly by measuring % water. We found that the energy density of herring varied markedly between years, in a surprisingly close relationship with productivity of the seabirds until 2000, after which seabird productivity and energy density of herring became uncoupled (Figure 10) so that the two were no longer correlated significantly (Figure 11). After 2000, herring was no longer the predominant prey item in any of the seabirds,

so the breeding success of seabirds was no longer driven by, or a good indicator of, the condition of the herring.

4.2. LARVAL ABUNDANCE

It would be reasonable to expect that the availability of 0-group herring to seabirds in the summer would be positively related to the abundance of herring larvae produced the previous fall and early winter. To test this we regressed % herring in the diet of each species of seabird on the herring larval survey from the previous year (Dr. R. Stephenson, Dept. of Fisheries and Oceans Canada, *in litt.*). The regression was not significant in either puffins or razorbills, but in both terns there was a significant but *negative* relationship, i.e. high larval counts were followed by low % herring in tern diet, and *vice versa* (Figure 12).

5. Discussion and General Conclusions

Weather, as expected, was wetter and more temperate at MSI than on the nearby mainland; summers on the island are cooler, windier, wetter, and with more variable rainfall but more equable temperatures (higher minima, lower maxima) than on the mainland. We conclude that it is necessary to measure weather locally rather than rely on data from more distant recording stations.

Although average SST values during the summer at MSI were similar to those in the surrounding region, the within-season pattern was different; SST was warmer at MSI in spring but colder in late summer, i.e. the water warmed up much less during the summer around the island than it did regionally. We do not know, in general, whether the seabirds respond more to the local than the regional SST; this question requires further research. However the scale of response by puffins – at least as reflected in their laying dates – apparently crosses the north Atlantic. Puffin laying dates were not related to local SST over the 8 years we measured them, and both laying dates and SST were outside the range covered by the Norwegian data with which we compared them; Norwegian SST varies between 3 °C and 5 °C in May (Barrett, 2001), compared with 6–7 °C at MSI (Figure 6). When MSI data are plotted on the same graph as Norwegian data, we see that they are in fact consistent; the regression line describing the Norwegian and MSI data combined explains nearly twice the variation explained by the line through the Norwegian data alone (r^2 0.59 and 0.32, respectively) (Figure 6). Thus our question ‘over what spatial scale do puffins respond (in laying date) to their marine environment?’ receives the quite unexpected answer ‘at the scale of the entire north Atlantic’.

This study has detected a statistically significant relationship in 6 of the 8 years between seabird productivity and the condition (fat content) of their major prey. This is a new result with no precedent in the seabird literature. Our previous work had shown some predictive relationship between arctic tern diet and the nearby herring fishery on Grand Manan; the present work shows a new relationship between

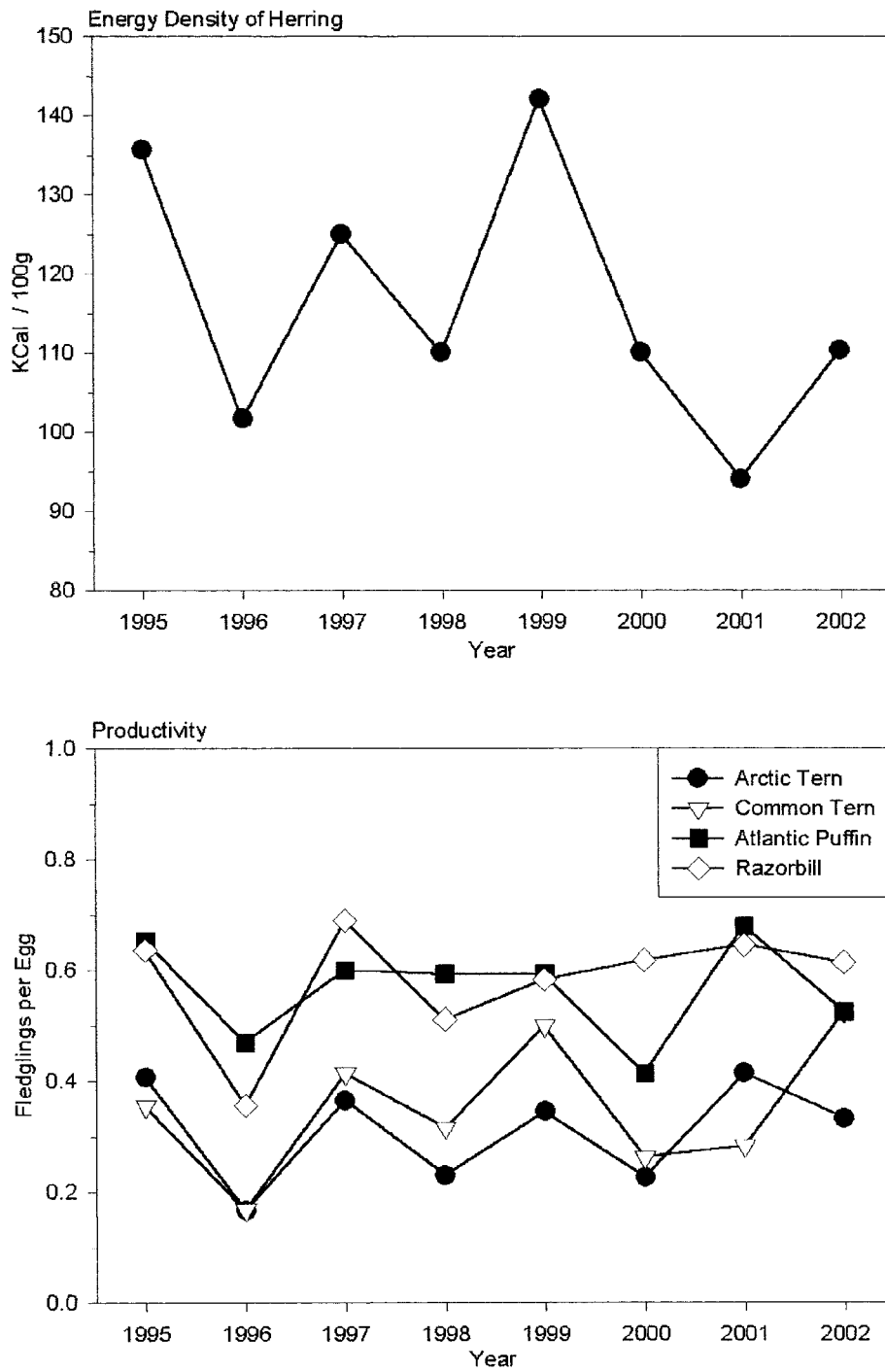


Figure 10. Relationship between annual productivity of four species of seabird and energy density of 0-group herring in diet, Machias Seal Island, 1995–2002.

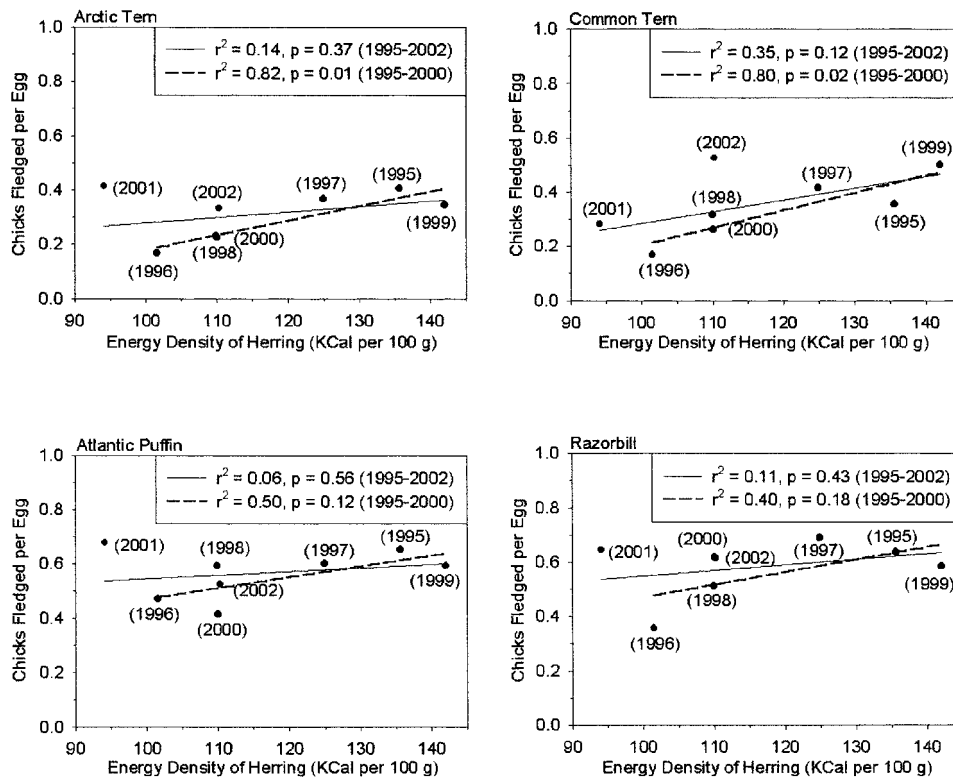


Figure 11. Correlations between annual productivity of seabirds and energy density of 0-group herring in diet, Machias Seal Island, 1995–2002. Regression lines and equations show change in relationship after the year 2000.

herring larval surveys and seabird diet. This is a further link in the seabird/herring chain, which we continue to pursue. More intriguing still is the strong negative correlation (in terns but not auks) between the preponderance of herring in the seabird diet and the abundance of larval herring in the previous fall, suggesting strong density-dependent competition among herring larvae such that more survive from small spawnings than from large ones. We suggest this as a possible topic for future research on herring biology, in which seabird dietary studies could provide samples of an age-class of herring ('0-group') that is currently not sampled at all by conventional fisheries techniques. In the two most recent years of this study, the decline of herring in seabird diet appears to have shifted to an alternative state in which herring comprises such a small part of the diet that its quality (energy density) no longer influences the breeding success of the seabirds. It remains to be seen whether this becomes a long-term regime shift, or is a short-term change in prey availability that will be reversed in future years. Even if the change proves to be transitory, it has acted fortuitously to confirm our preliminary hypothesis that

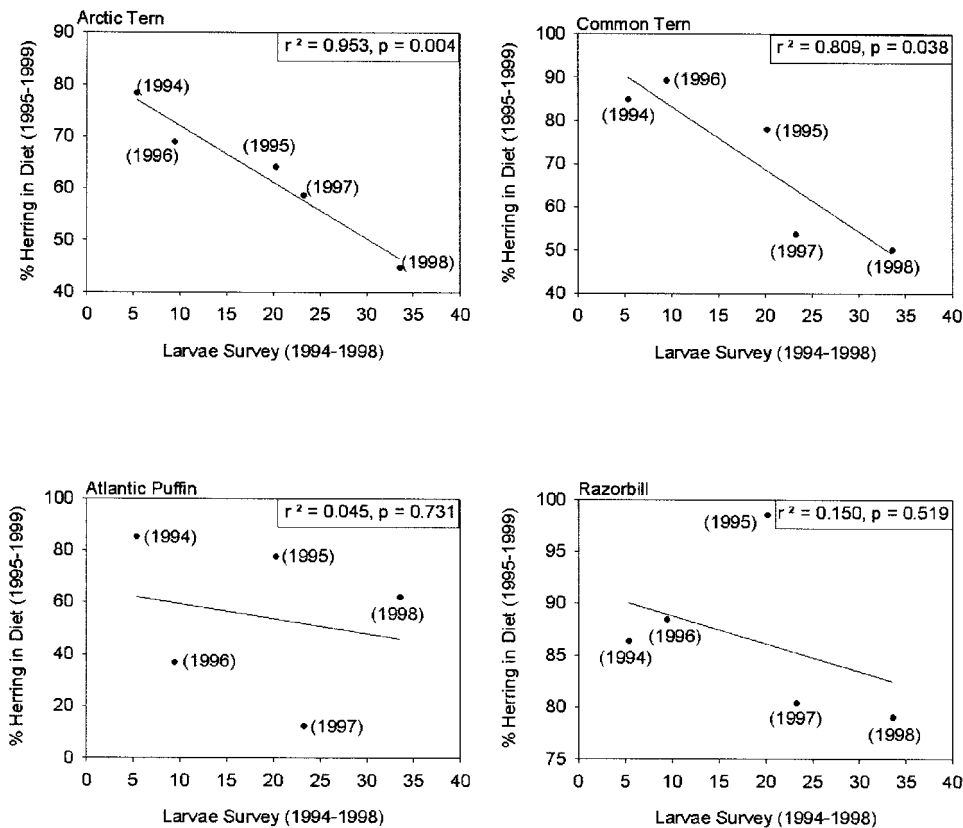


Figure 12. Relationship between larval counts of herring in the southern Bay of Fundy, and % herring in diet of seabirds Machias Seal Island the following summer.

the quality of the major prey has a strong influence on the success of at least some of the seabirds.

At this point we cannot answer the question ‘which seabird best reflects/predicts significant changes in the system?’ because there are significant differences in response among the four species under investigation. At present the strongest relationships we have found have been in the diet of arctic terns, and laying date of puffins. We expect that different seabird species, when we understand them better, will tell us different things about changes in the marine ecosystem, but we are still in the early stages of acquiring the understanding to define those relationships. The close relationship between the productivity of several species, and the quality of their main prey, adds another dimension to studies of predator-prey relationships in seabirds and identifies another link in the chain connecting seabirds, as top predators in marine ecosystems, with factors affecting energy transfer through marine food-webs.

Traditional population monitoring programs for seabirds focus on measuring trends in the numbers of breeding birds (e.g., Drury, 1973–1974; Hatch *et al.*,

1994). This information is necessary, but not sufficient, to ensure the sustainability of seabird populations; any trends detected will need to be linked to causative factors if appropriate action is to be taken. Our long-term research on Machias Seal Island follows the approach recommended by Marzluff and Sallabanks (1998) in combining systematic monitoring, of both environmental and seabird parameters, with focused, short-term studies carried out by a succession of graduate students addressing specific components of the overall research goal of understanding how seabirds respond to changes in their environment. Specifically, we want to be able to identify the environmental *causes* of the demographic and behavioural *responses* we see in the seabirds. Our work is incorporated into the regional seabird monitoring program of the Canadian Wildlife Service (Chardine, 1999) and indicates progress towards a truly integrated ecological approach to monitoring seabirds which will provide new understanding of the marine ecosystem as well as contributing to the conservation of seabirds.

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