

Changes in Canadian seabird populations and ecology since 1970 in relation to changes in oceanography and food webs

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Abstract: Systematic monitoring of seabird populations in Canada has been ongoing since the 1920s and the monitoring of diets and other biological indicators of ecosystem change started in the 1970s. Long-term monitoring of population parameters began in the 1980s. These studies originally were conducted mainly by the Canadian Wildlife Service, but subsequently have involved several universities and nongovernment organization groups. We review the results of this monitoring from the 1970s onwards for six oceanographic regions to assess population trends among Canadian seabirds and correlated trends in diets, phenology, and other breeding biology variables. Within regions, trends in most variables studied have been broadly congruent, but there was often variation among regions. In particular, seabird populations in the Pacific coast zone affected by the California Current upwelling system have shown generally negative trends since the 1980s, whereas trends for populations of the same species to the north of this zone have been mainly positive. Likewise, on the east coast, trends at Arctic colonies have been decoupled from those at colonies around Newfoundland and in the Gulf of St. Lawrence, especially since the major cold water event of the early 1990s. Several long-term studies have shown an association between population events and diet and phenology changes. Diet and indicators of condition (chick growth, reproductive success) sometimes responded very rapidly to oceanic changes, making them excellent signals of ecosystem perturbations. The review highlights the effects of decadal-scale regime shifts on Canadian seabirds, confirms the value of long-term studies and supports the applicability of single-site observations to regional populations.

Key words: seabirds, Canada, oceanography, population trends, environmental monitoring, regime shift, indicators.

Résumé : Au Canada, le suivi systématique des populations d'oiseaux marins s'effectue depuis les années 1920 et le suivi des diètes et autres indicateurs biologiques de changement des écosystèmes, depuis les années 1970. Le suivi à long terme des paramètres des populations a débuté dans les années 1980. Ces études ont été conduites au départ par le Service canadien de la faune, mais subséquemment ont impliqué plusieurs universités et groupes d'organisations non gouvernementales. Les auteurs passent en revue les résultats de ces suivis à partir des années 1970 en continu pour six régions géographiques, afin d'évaluer les tendances des populations chez les oiseaux marins canadiens et faire des corrélations avec les diètes, la phénologie et autres variables de la biologie de l'accouplement. Dans les régions, les tendances pour la plupart des variables étudiées se sont avérées largement congrues, mais on observe souvent une variation entre les régions. Particulièrement, les populations d'oiseaux marins de la zone côtière du Pacifique, affectées par le système de dérive du courant de Californie, montrent des tendances généralement négatives depuis les années 1980, alors que les tendances pour les populations des mêmes espèces au nord de cette zone se sont avérées généralement positives. De la même façon, sur la côte

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est, on observe des tendances vers un découplage des colonies arctiques par rapport aux colonies de Terre-Neuve et du golfe St-Laurent, surtout depuis l'arrivée majeure d'eau froide dans les années 1990. Plusieurs études à long terme ont montré une association entre les événements dans les populations et les changements de diète et de phénologie. La diète et les indicateurs de conditions (croissance des jeunes, succès de la reproduction) réagissent quelques fois très rapidement aux changements océaniques, ce qui en fait d'excellents signaux de perturbation des écosystèmes. Cette revue souligne les effets des changements de régime à l'échelle des décades chez les oiseaux de mer canadiens, confirme l'intérêt des études à long terme et supporte l'applicabilité d'observations sur des sites individuels aux populations régionales.

Mots-clés : oiseaux marins, Canada, océanographie, tendances des populations, suivis environnementaux, changements de régime, indicateurs.

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Introduction

Tracking bird populations to monitor environmental change has frequently been advocated (Furness and Greenwood 1993). Because of the expense and technical difficulty of sampling marine resources, especially offshore, seabirds present an especially attractive option for monitoring marine environments (Cairns 1987; Vermeer 1992; Piatt et al. 2007; Wanless et al. 2007; Parsons et al. 2008). Seabirds are ubiquitous and wide-ranging, many species are readily observed and counted and they feed over many trophic levels including plankton, small and large pelagic fishes, and squid (Montevecchi 1993; Diamond and Devlin 2003). Colonial species often travel long distances to feed but return at regular intervals to a central breeding site, so that colony-based studies can integrate data over large marine areas (Diamond 1978; Cairns 1987; Parsons et al. 2008). Consequently, observations of changes in seabird ecology can provide practical and sensitive indicators of changes in marine ecosystems. Information from seabird monitoring contributes increasingly to ecosystem-based fisheries management (Eiender 2009).

Links between stocks at lower trophic levels and changes in seabird populations and biology, especially reproduction, have been demonstrated for many species and regions (e.g., Nettleship et al. 1984; Monaghan et al. 1989; Hatch and Sanger 1992; Bertram and Kaiser 1993; Ainley et al. 1995; Montevecchi and Myers 1996; Bryant et al. 1999; Tasker et al. 2000; Hedd et al. 2002, 2006; Davoren and Montevecchi 2003; Baillie and Jones 2004; Deguchi et al. 2004; Frederiksen et al. 2005; Mallory 2006; Furness 2007; Thayer et al. 2008). Among a variety of biological indicators commonly monitored for marine birds, the following are particularly useful for assessing the state of the ecosystem (Cairns 1987; Boyd and Murray 2001):

- (1) population trends — an integrated signal, usually based on breeding numbers and responding to ecosystem states over multiple years;
- (2) changes in diet, especially nestling diets — indicators of changes in food web structure over periods of days to decades;
- (3) changes in timing of breeding — a potential indicator of changes in climate or oceanic processes that drive phenological change at lower trophic levels;
- (4) egg and clutch size, nestling growth and reproductive success — indicators of food availability to breeding

birds and hence how hard parent birds need to work in a specific year;

- (5) changes in attendance patterns, either duration of attendance, or numbers of birds attending at one time — indicators of day-to-day variation in conditions, as well as inter-year changes;
- (6) changes in breeding, foraging and migratory distribution — multi-year indicators of large-scale and persistent change.

The value over different time-scales of different seabird indices has been investigated by Boyd and Murray (2001), Gill and Hatch (2002), and Gill et al. (2002). For many species, only the breeding segment of populations is assessed (through counts of nests or breeders attending sites), so factors that affect the proportion of the total population breeding potentially complicate relationships between population trend and changes in the marine environment. However, in most years at most sites, the proportion of the population breeding does not vary by more than a few percent. Years in which higher than normal numbers of breeding age birds refrain from breeding tend to stand out as unusual in other respects (e.g., egg desertion, high chick mortality) and such years are eliminated from analysis of population trends. In fact, breeding population, total population attending breeding sites and total population size, can all provide information on environmental change, although the latter is difficult to measure and the breeding population size may lag environmental change by several years (Gill et al. 2002).

Long-term studies of seabird populations, diet and breeding biology based at breeding colonies have been ongoing in Canada since the 1920s. Originally most of this work was conducted by the Canadian Wildlife Service (formerly the Dominion Wildlife Service), but since the 1970s there has been an increasing involvement by universities and nongovernmental organizations. Information for eastern Canada up to the mid-1970s was reviewed by Nettleship (1979) who laid out a blueprint for ongoing monitoring. In this paper we assess the progress made in seabird monitoring in Canada since 1970. We review trends in monitoring indices for a variety of seabirds throughout Canadian waters and compare these trends with major environmental changes observed over the period considered. In addition, we deal mainly with colonial-breeding species, as these are generally easier to study and therefore we have more complete information for them.

In deciding how much attention to devote to different species, we have used the following criteria in assessing their value as ecosystem indicators:

- (1) Are species abundant and characteristic of the given zones? Populations comprising less than 200 breeding pairs at some time during the period considered are generally omitted because the dynamics of small populations are strongly affected by immigration and by stochastic processes.
- (2) Do we have data on populations for which counts or other biological indicator data are available going back to at least 1993 (15 years)?
- (3) Where possible, are species or populations relatively unaffected by terrestrial problems created by human activities, such as logging, garbage dumps, or introduced predators on breeding colonies?
- (4) We concentrate on the evidence for ecosystem changes provided by seabird populations and biology, rather than speculating on the potential consequences for seabirds of ecosystem changes determined from other evidence.

Population changes integrate information on survival over the entire year. For species that migrate away from their breeding areas population trends may reflect conditions in both nonbreeding and breeding areas. Consequently, population changes of migratory species are less useful for assessing conditions in a specific zone than those of sedentary species or local migrants, though they can be useful for assessing broader scale environmental patterns. As most seabirds are migratory, or disperse widely away from their breeding sites during winter (Löfgren 1984; Gaston 2004), some consideration of potential wintering area effects are required for most data sets.

In the Atlantic, especially around Newfoundland and Labrador and in the Gulf of St. Lawrence, a major food-web disruption occurred around 1990, coinciding with over-fishing that led to the closure of the ground-fishery off eastern Canada and the cod fishery moratorium on the North Shore of the Gulf in 1992 (Hutchings and Myers 1994; Montevecchi and Myers 1996). The disruption was associated with anomalously low water temperatures and salinity in the early 1990s (see Colbourne 2004), reduction in important zooplankton species (Sameoto 2004), reduced cod recruitment and growth (Mann and Drinkwater 1994), later capelin spawning and a reduced fish size, and shift by capelin to more offshore areas and to deeper water (Carscadden et al. 2001; Mowbray 2002). For that zone, trends have been split between pre- and post-1990. Repercussions of this major event for seabirds have been noted by Montevecchi and Myers (1996, 1997), Regehr and Rodway (1999), and Rowe et al. (2000).

On the Pacific coast, two major “regime shifts” relating to the Pacific Decadal Oscillation (PDO; Hare and Mantua 2000) are recognised during the period we are considering. These occurred in or about 1977, 1989 and perhaps 1998 and involved the degree of upwelling occurring in the California Current system, as well as related events throughout the North Pacific. Repercussions for seabirds have been extensively documented further south (Ainley et al. 1995; Sydeman et al. 2001; Hyrenbach and Veit 2003).

Descriptions of many of the phenomena described here have been published previously, although over shorter time series. Details of unpublished data sets are available through the PSG Seabird Monitoring Database (<http://www.absc.usgs.gov/research/psinfonet/psmdb/splashpsmdb.htm>), which also describes protocols for the observations. In dealing with population trends, most analyses are based on index counts of selected colonies and (or) study areas. Approximate population sizes can be obtained from the relevant regional summaries (Brown et al. 1975; Rodway 1991; Vermeer et al. 1993; Lock et al. 1994; Vermeer and Morgan 1997; Latour et al. 2008)

Methods

Zonal definitions

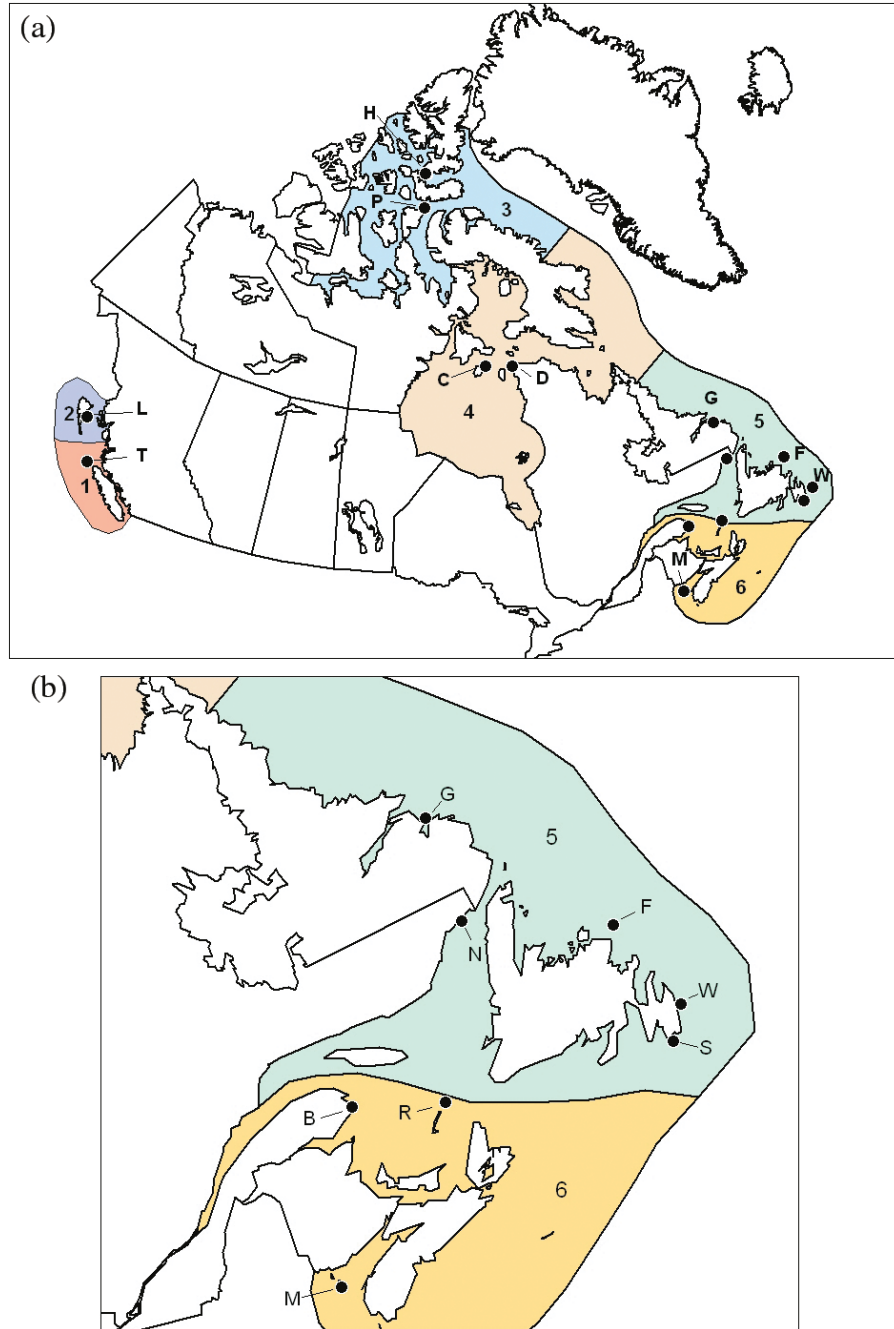
For the Pacific coast, we have divided studies into those carried out within the California Current upwelling zone — roughly the outer coast north to Queen Charlotte Sound (zone 1, Fig. 1) — and those in more northern waters (zone 2). For the Arctic, we considered the High and Low Arctic (as defined by Dunbar 1972) separately (zones 3 and 4) and for the Atlantic coast we considered Newfoundland and Labrador and the northern Gulf of St. Lawrence (zone 5) separately from the waters of the southern Gulf, Scotian Shelf, and Bay of Fundy (zone 6). We have not considered trends within the Strait of Georgia (very little work conducted since 1980s), where all seabird populations are affected by a wide range of human activities (Vermeer and Butler 1994), or in the Beaufort Sea, where few colonial seabirds breed and where, consequently, little information on seabirds is available (Alexander and Hawkings 1988; Alexander et al. 1991).

Population monitoring

The location of the breeding colonies where monitoring has been carried out is shown in Figs. 1a and 1b. Detailed descriptions of methods are given in the relevant references. Census methods vary among species, but broadly divide into (1) direct counts, made either on the ground or from photographs, of surface-nesting birds (Northern Fulmar *Fulmarus glacialis*, Northern Gannet *Morus bassanus*, cormorants *Phalacrocorax* spp., gulls *Larus* spp., Black-legged Kittiwake *Rissa tridactyla*, terns *Sterna* spp., murre *Uria* spp.) and (2) sampling surveys based on transects or randomly placed study plots carried out for sub-surface nesters (storm-petrels *Oceanodroma* spp., various auks *Alca*, *Fratercula*, *Cerorhinca*, *Ptychoramphus*, *Synthliboramphus*). For burrow-nesters, often burrow entrances are counted and only a sample of these inspected for occupancy (the presence of a breeding bird), in which case nest densities are a product of burrows × occupancy.

Population trends are monitored either by repeat censuses of entire breeding populations (e.g., Northern Gannet; Nettleship and Chapdelaine 1988), or by periodic counts of nests or individual birds on permanent monitoring plots, usually covering only a small portion of the total population and following a variety of protocols (e.g., Thick-billed Murre *Uria lomvia*, Gaston 2002; Atlantic Puffin *Fratercula arctica*, Rodway et al. 2003). A few species are monitored away from the breeding site, as is the case for the solitary-nesting

Fig. 1. (a) Map of Canada, showing the approximate boundaries of the zones used and the location of important colonies mentioned in the text: C = Coats Island, D = Digges Island, F = Funk Island, G = Gannet Islands, H = Hell Gate and Cape Vera, L = Laskeek Bay and Reef Island, M = Machias Seal Island, P = Prince Leopold Island, T = Triangle Island, W = Witless Bay; (b) Detail showing the location of seabird colonies mentioned in Atlantic Canada and the Gulf of St. Lawrence: B = Bonaventure Island, F = Funk Island, G = Gannet Islands, M = Machias Seal Island, N = North Shore, Gulf of St. Lawrence, R = Bird Rocks (Rochers aux Oiseaux), S = Cape St. Mary's, W = Witless Bay.



Marbled Murrelet *Brachyramphus marmoratus*, where replicated counts at sea or of birds in flight captured on marine radar (Burger 2001) have been used to assess population trends (Piatt et al. 2006). This species will not be included here because population trends are likely driven by the effects of commercial timber extraction on breeding habitat.

Monitoring breeding biology

Reproductive timing and success, nestling growth rate and diet are monitored by a wide range of methods. Studies of reproduction mostly involve periodic inspections of breeding sites to record egg-laying and the progress of breeding. This can be done without disturbance to nesting birds by remote

observations of surface-nesting sites, or by generally more intrusive investigation of crevice or burrow nests. Nestling growth may be measured by weighing nestlings during these site inspections, but more commonly nestling growth is measured at sites other than those used to monitor reproduction, as periodic weighing can affect reproductive success (Gaston 1985). Diet may be measured by obtaining regurgitations from a sample of nestlings or from adults delivering food to them (e.g., storm-petrels, Hedd and Montevecchi 2006; Northern Gannet, Montevecchi and Myers 1996; cormorants, Seefelt and Gillingham 2006; Cassin's Auklet *Ptychoramphus aleuticus*, Vermeer 1981, 1985; Rhinoceros Auklet *Cerorhinca monocerata*, Hedd et al. 2006). For some species, food delivered can be observed and accurately recorded from a distance, without disturbance to the birds (e.g., murre, Gaston et al. 2003; Razorbill *Alca torda*, Chapdelaine and Brousseau 1996; Atlantic Puffin, terns, Diamond and Devlin 2003; Clarke et al. 2008). In all cases, data are based on observations or samples from relatively small proportions of the populations concerned.

Results

Zone 1: Pacific coast north to central Queen Charlotte Sound, including the Scott Islands off northern Vancouver Island

Breeding populations of marine birds in the southern part of this zone are generally small and scattered and have not been tracked intensively. Baseline data are available for all seabird colonies in British Columbia (BC) from surveys carried out in 1970 by the BC Provincial Museum (Rodway 1991), but estimates for most large colonies were very approximate. The largest colony in this zone is at Cleland Island, Clayoquot Sound (Vermeer et al. 1992). Data on Rhinoceros Auklet breeding and diet are also available from Seabird Rocks (Bertram et al. 2002).

Seabirds in the northern part of this zone are heavily concentrated on Solander Island and the three outer Scott Islands, Beresford, Sartine, and Triangle. Triangle Island is the most important seabird colony in BC and is the site of the most intensive seabird monitoring programme in Canada. Monitoring of seabird diets and reproductive success there was initiated in 1976 (Vermeer et al. 1979; Vermeer and Cullen 1979) but was intermittent up to 1994, since when it has been annual and implemented in collaboration between Simon Fraser University and the Canadian Wildlife Service. A full census of most species was not carried out until 1982 (Rodway et al. 1990). Population monitoring is based on a small number of years only and is therefore much coarser in scale than monitoring of breeding biology. Good data on the indicator species are available mainly from the late 1970s and 1980s onwards for Common Murre *Uria aalge*, Rhinoceros Auklet, Cassin's Auklet, and Tufted Puffin *Fratercula cirrhata* at Triangle Island.

Results from the Triangle Island work form the backbone to our understanding of seabird-ecosystem processes on the West Coast. Significant changes in diet, timing of breeding, adult survival, and reproductive success have been demonstrated for Common Murre, Rhinoceros Auklet, Cassin's Auklet, and Tufted Puffin during the period from 1976 onwards. The variation is related to large-scale oceanic

changes affecting sea surface temperature and the timing and intensity of upwelling in the northernmost part of the California Current system. This affects the availability of prey species within range of the colony during the critical breeding period.

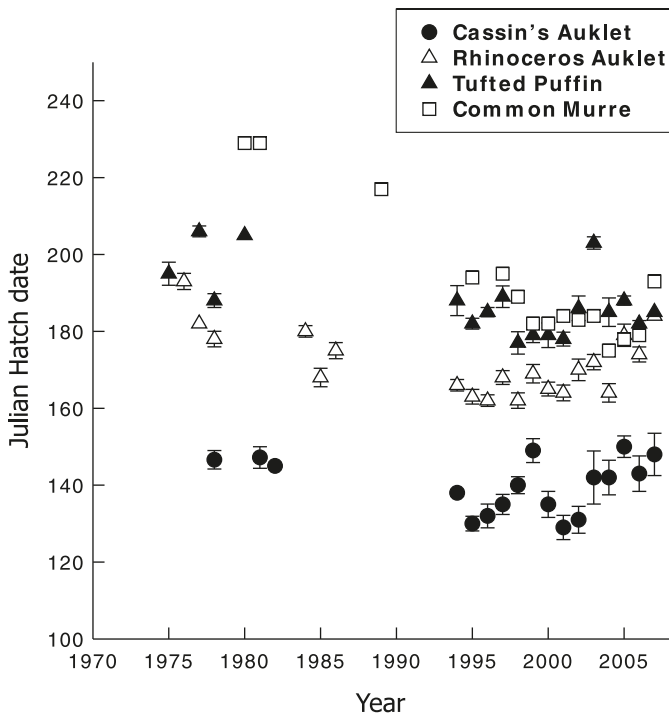
Population trends

At Triangle Island, burrow counts of all three burrow-nesting auks within study plots declined between 1984 and 2004: Rhinoceros Auklets by $-0.2\%/year$, Cassin's Auklets by $-2.3\%/year$ and Tufted Puffins by $-1.7\%/year$. Some levelling off was observed for Cassin's Auklets in 1999–2004 (MJFL and JM unpublished data), but 2005 was the worst year on record for the breeding of this species at Triangle Island (Sydeman et al. 2006) and the population certainly has declined further, although the magnitude of the change is not known (JM unpublished data). Counts of Common Murres also suggest a decline in population by $2.2\%/year$ between 1989 and 2003, and an abandonment of several satellite colonies. However, these are based on total birds counted rather than occupied sites or breeding pairs, and may reflect behavioural responses of murre to increased disturbance by an expanding population of Bald Eagles *Haliaeetus leucocephalus* rather than demographic responses to ocean climate variability (Hipfner 2005).

Biological indicators

Timing of breeding of all species at Triangle Island advanced between the late 1970s and late 1990s (Fig. 2), although there was much interspecific and interannual variation (Bertram et al. 2001). The mean date of hatching of Tufted Puffins was approximately 15 July during 1975–1981, but ranged from 22 June to 10 July after 1994 (Gjerdrum et al. 2003). For Common Murre the advance in timing of breeding was even more dramatic with chicks not hatching until early August in the 1980s, but advancing by more than a month by the 1990s (Hipfner and Greenwood 2008). Nestling growth and survival of Tufted Puffins and Rhinoceros Auklets, both of which feed their nestlings primarily on fish, was poor during the 1990s compared to the 1980s and the period from 1999 to 2001, with few nestlings reared in 1994 and 1996–98 (Gjerdrum et al. 2003; Hedd et al. 2006). Breeding success and nestling growth have remained variable for both species through mid-2000s, including near-complete colony failure for Tufted Puffins during the mild El Niño event in 2003 (Hipfner et al. 2007, 2008). In general, poor growth conditions for both species are associated with warm sea surface temperatures (SST), which are related to poor recruitment of 0+ sand lance *Ammodytes* spp. (Hedd et al. 2006) and minimal representation in nestling diets (Fig. 3). Recent observations indicate how strong and rapid these species' responses to ocean climate can be: in 2007, a year of very weak marine primary production, many Rhinoceros Auklets did not breed and those that did experienced their worst breeding season in 20 years of records at Triangle Island. Tufted Puffins experienced near total breeding failure ($<10\%$ successful). In 2008, a year of cold ocean conditions and very strong marine primary production, both of these species experienced their best breeding season, in terms of chick growth rates and fledging masses (JM unpublished data).

Fig. 2. Mean dates of hatching ($\pm 95\%$ conf. intervals) for Cassin's Auklet, Rhinoceros Auklet and Tufted Puffin, and dates of first hatching for Common Murres at Triangle Island since 1975 (from Gjerdrum et al. 2003; Hipfner and Greenwood 2008; JMH unpublished data).



For the more zooplanktivorous Cassin's Auklet, studies at Triangle Island indicate that annual breeding success is largely determined by the degree of temporal matching between the birds' chick-provisioning period and the period during which the subarctic copepod *Neocalanus cristatus* is available to them in near-surface waters (Bertram et al. 2001). In cold, late years, the period of maximal biomass of late-stage copepodites in near-surface waters begins late and ends late, matching well with the birds' energetically demanding chick-provisioning period, while in warm years, the peak occurs too early and spans too narrow a window of time for the birds (Hipfner 2008). Offspring growth and survival are strongly affected by the amount of *N. cristatus* they receive from their parents while in the nest (Fig. 4).

During 1994–2000, annual adult survival of Cassin's Auklets at Triangle Island was only 71%, compared with 80% at Frederick Island, off west coast Haida Gwaii over the same period. Both colonies experienced reduced adult survival during the intense 1997–98 ENSO event (Bertram et al. 2005). The difference in survival rates between the two colonies, along with negative population trends at Triangle and nearby Sartine islands (JMH and MJFL unpublished data), suggests that conditions at the northern extent of the California Current upwelling zone were sub-optimal for auks during the 1990s. As in other auks, breeding success of Cassin's Auklet at Triangle Island varied between 2000 and 2005 with very good years (2004, mean chick departure mass 170 g) and very poor years (2005, complete breeding failure; Wolf et al. 2009). This observation is similar to observations of this species elsewhere in the California Current

system (Ainley et al. 1995; Sydeman et al. 2001; Lee et al. 2007). Conversely, conditions for reproduction in the downwelling zone off the west coast of Haida Gwaii seem to have been little affected: nestling growth rates were generally good throughout the period for which we have data (1995–1998). This was made most apparent in 2005, when Cassin's Auklet suffered a near complete breeding failure at Triangle Island (Sydeman et al. 2006), yet success was very good at Frederick and Rankine islands in Haida Gwaii (JMH and MJFL unpublished data; Bertram et al. 2009). Overall, it appears that conditions for Cassin's Auklet and probably for Rhinoceros Auklet reproduction as well, are much more variable at Triangle Island than at colonies in zone 2, where both species have been uniformly successful over the period on record.

Zone 2: Pacific coast north of Queen Charlotte Sound, including Hecate Strait

Aside from the early mapping by the BC Provincial Museum, seabird monitoring in this zone dates only from the 1980s, with extensive surveys carried out by the Canadian Wildlife Service during 1980–1987 (Rodway et al. 1988, 1990; Rodway 1991). Good data are available for population size, timing of breeding, and reproductive success for Ancient Murrelet *Synthliboramphus antiquus* and Cassin's Auklet at colonies in Haida Gwaii. Scattered data are available for a few colonies elsewhere on the North B.C. coast, e.g., Lucy and Pine islands, both large Rhinoceros Auklet colonies (Bertram and Kaiser 1993).

In contrast to observations at Triangle Island, most burrow-nesting auks breeding in Haida Gwaii (Queen Charlotte Islands) increased in numbers since the 1980s (MJFL, JMH, and AJG unpublished data; Fig. 5), with very high rates of increase of Ancient Murrelets at Reef Island, in Laskeek Bay (6.6%/year from 1985 to 1995) and for Rhinoceros Auklets at Skaang Gwaii (4.3% per year from 1985 to 2006). Elsewhere in this zone, the Rhinoceros Auklet population on Lucy Island, near Prince Rupert, increased by 1.7%/year between 1984 and 2006 (MJFL and JMH unpublished data; Fig. 5).

Ancient Murrelets have increased on all colonies monitored in Haida Gwaii (their only breeding area in Canada) where they have not been subjected to introduced predators, while Cassin's Auklets have shown small declines in the same region (Regehr et al. 2007; Fig. 5). This is despite evidence that, in northern waters, the two species both feed on zooplankton in summer (Sealy 1975; Vermeer et al. 1987; Burger and Powell 1990). However, their wintering habits differ, with Cassin's Auklets wintering further south and offshore, near the shelf-break (Briggs et al. 1987), while Ancient Murrelets winter in large numbers among inshore areas subject to tidal upwelling (Gaston et al. 1993). Hence, the difference in their population dynamics could be driven by factors operating outside the breeding season. Alteration of Cassin's Auklet breeding habitat due to forest blowdown and spruce regeneration may also be involved (MJFL and JMH unpublished data).

The timing of breeding in Laskeek Bay, where Ancient Murrelet breeding biology has been monitored since 1985, has become earlier since the 1980s, but only by a few days.

Fig. 3. Proportion of three major prey species (% bill loads) in the diet of nestling Rhinoceros Auklets at Triangle Island 1976–2001 (adapted from Hedd et al. 2006).

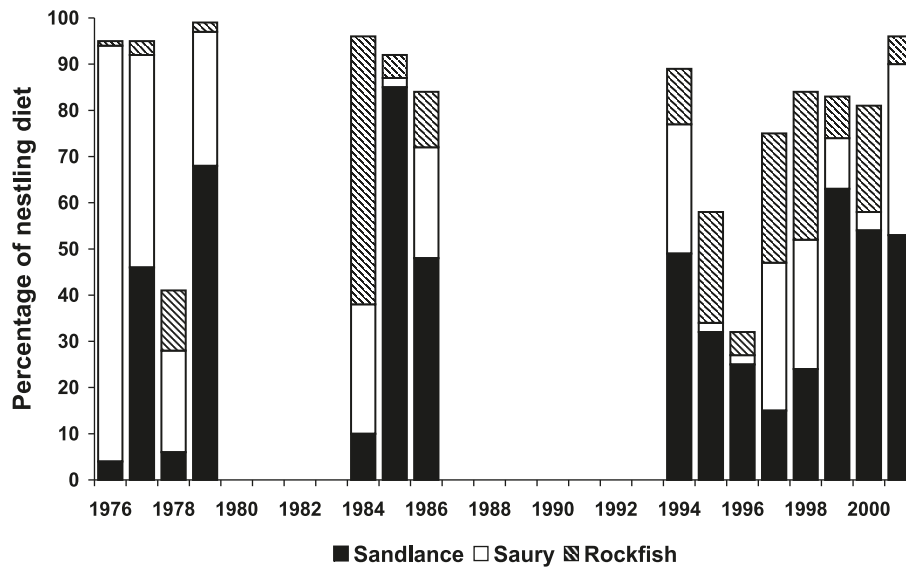
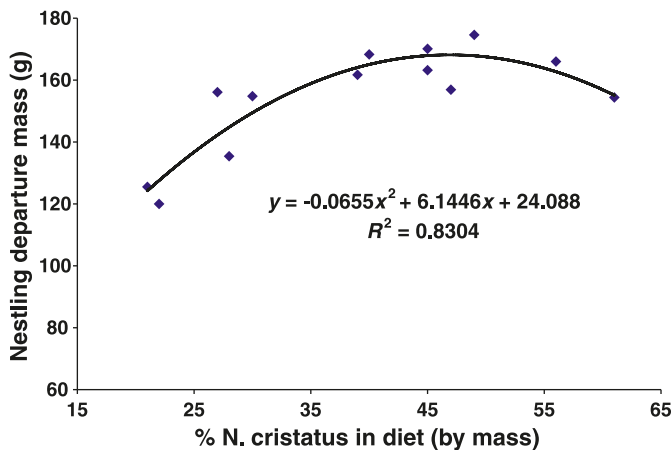


Fig. 4. Cassin’s Auklet nestling departure mass at Triangle Island during 1996–2008 in relation to the proportion of *Neocalanus cristatus* in their diet (mean proportion by wet weight). For details see Hipfner (2008).



Despite this trend 2007 was the latest year on record (Gaston 2008).

The population of Ancient Murrelets in Haida Gwaii is currently significantly depressed by predation by introduced mammalian predators (Gaston 1992; Bertram and Nagorsen 1995). However, subsequent to eradication of rats from Langara Island in 1995, the population there doubled between 1998 and 2004 (+13%/year; Regehr et al. 2007). This rapid recovery suggests that ecological conditions around Langara Island remain highly suitable for Ancient Murrelets.

Zone 3: Eastern High Arctic from northern Baffin Island and Devon Island to Bathurst Island and the Queen Elizabeth islands

Data on diet and population trends for Thick-billed Murres, Northern Fulmars, Black-legged Kittiwakes, and Glaucous Gulls *Larus hyperboreus* are available since 1975 from Prince Leopold Island, situated in Barrow Strait. Popu-

lation trend data are available for Northern Fulmars at Cape Vera, Devon Island. Additional data are available on Ivory Gulls *Pagophila eburnea* and Black-legged Kittiwakes at several colonies.

At Prince Leopold Island several species showed changes in timing of breeding, reproductive success, and adult colony attendance in response to variation in ice conditions since 1975 (Gaston et al. 2005a). Figure 6 illustrates this relationship for timing of breeding in Thick-billed Murres: trends are similar for Black-legged Kittiwakes and Glaucous Gulls. Overall population trends since 1970s were positive for both Thick-billed Murres (+3.0%/year to 1988, no significant change subsequently) and Black-legged Kittiwakes (no significant change from 1975 to 1988, +3.4%/year from 1988 to 2008, Fig. 7). Northern Fulmars showed great inter-year variation in colony attendance. Numbers at Prince Leopold Island decreased at 1.0%/year from 1976 to 2008 (Fig. 7). Although evidence is sparse, several Northern Fulmar colonies in this zone (the only one in Canada where Northern Fulmars are abundant) show signs of declining (Gaston et al. 2006). There is also evidence that Glaucous Gull numbers have declined by >50% since the 1970s, but the numbers of birds and colonies monitored are small (AJG and H.G. Gilchrist unpublished data). Intermittent censuses of several kittiwake colonies suggest that their numbers have increased in the Lancaster Sound – Barrow Strait region since the 1970s (Mallory et al. 2009; Fig. 7).

The population of Ivory Gulls breeding in northern Nunavut (northern Baffin Island, Devon Island, and southern Ellesmere Island), formerly about 2000 pairs, fell by >80% between the 1980s and 2005 (Gilchrist and Mallory 2005). Likewise, numbers seen at sea in the High Arctic, post-breeding, declined between 1993 and 2002 (Chardine et al. 2004). The speed of the decline, the remoteness of their breeding sites, and their tendency to shift among breeding sites from year to year have made it difficult to study the problem. Consequently, we do not know whether it was due to changes on the breeding grounds, or on their marine feed-

Fig. 5. Changes in populations of burrow-nesting auks in zone 1 (Triangle Island and zone 2 (all others) between the 1980s and 2000s, expressed as % annual change. N = species not present, or not monitored at that site (MJFL, JMH, AJG, unpublished data).

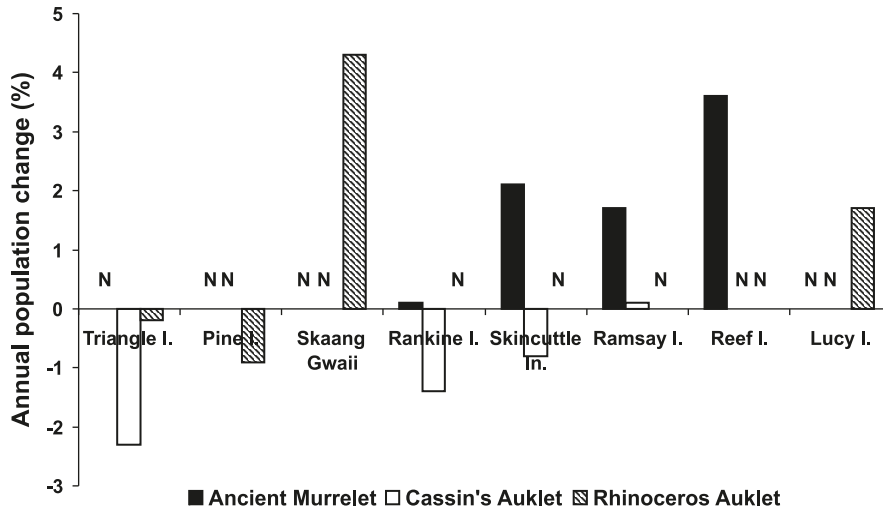
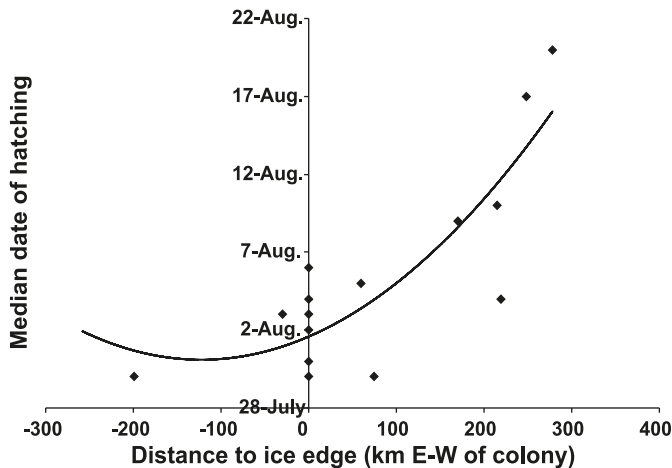


Fig. 6. Median date of hatching for Thick-billed Murres at Prince Leopold Island, Nunavut, in 13 years between 1975 and 2008 (adapted from Gaston et al. 2005b). Quadratic polynomial fit: $R^2 = 0.72$.



ing areas. The latter seems most likely, but the specific change that affected them is unknown.

The divergence in trends between Thick-billed Murres, Black-legged Kittiwakes, and Northern Fulmars at Prince Leopold Island (Fig. 7), where all three species feed similar food to their nestlings, principally Arctic cod *Boreogadus saida*, suggests that trends are determined by events on the wintering grounds, rather than in the vicinity of the colony. For Thick-billed Murres, similarity between trends in the High and Low Arctic have already been identified as a possible indicator of population control during the nonbreeding season (Gaston 2003).

Zone 4: Eastern Low Arctic from northern Labrador to Cumberland Sound, Baffin Island and including Hudson Strait, Hudson Bay, and Foxe Basin

Data on diet and population trends for Thick-billed Murres and Glaucous Gulls are available from Digges and

Coats islands (see map) from 1980 onwards. Information on population trends in gulls and Arctic Terns (*Sterna parasaea*) is available from islands in eastern Hudson Bay. Information available on populations elsewhere derives from only two to three visits.

Population trends

At Coats Island, where annual monitoring counts for Thick-billed Murres are available since 1985, the population has shown an overall increase of 1.7% annually, but this has been uneven, with a sharp decrease in 1989–1991, coinciding with the closure of the groundfish industry and the cold water event off eastern Newfoundland (where these birds winter), followed by rapid increase in the 1990s, levelling off after 2000 (Gaston 2002 and unpublished; Fig. 8). Trends have been similar at Digges Island and since 2000 both colonies have been stable, similar to Prince Leopold Island (Fig. 9). Glaucous Gulls have declined by approximately 50% in the Digges Sound region (AJG unpublished data) and farther south, in the Belcher Islands (Gilchrist and Robertson 1999), where Arctic Terns have also declined (–40% to –95% in different archipelagos between 1980s and 1997). No cause for Glaucous Gull declines has been identified.

Biological indicators

Breeding of Thick-billed Murres at Coats Island has become earlier since the 1980s, with an average advance of 6 d in the mean date of hatching. This compares with a 17 d advance in the date of ice break-up in adjacent waters (Gaston et al. 2009a). Timing of breeding by Glaucous Gulls is closely tied to that of Thick-billed Murres (Gaston et al. 2009b), the murre eggs and nestlings being the principal food fed to the young gulls where they breed in association with murres. Hence the date of laying of gulls has advanced in step with the murres. These effects are probably linked to climate change, especially the advance in the date of ice break-up in Hudson Strait and Hudson Bay (Gaston et al. 2009a).

Fig. 7. Trends in numbers of Thick-billed Murres, Black-legged Kittiwakes, and Northern Fulmars counted on population monitoring plots at Prince Leopold Island: baseline is mean of 1975–77 = 100. Lines are quadratic polynomial fits.

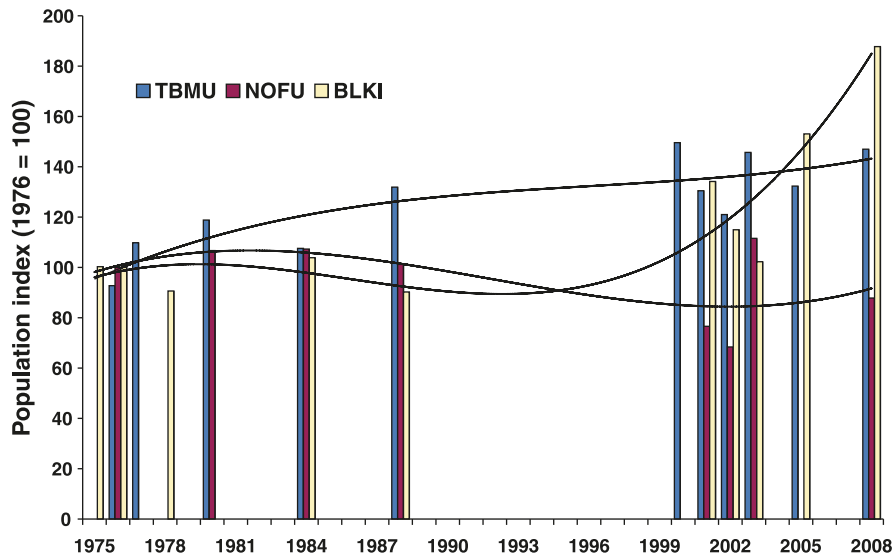
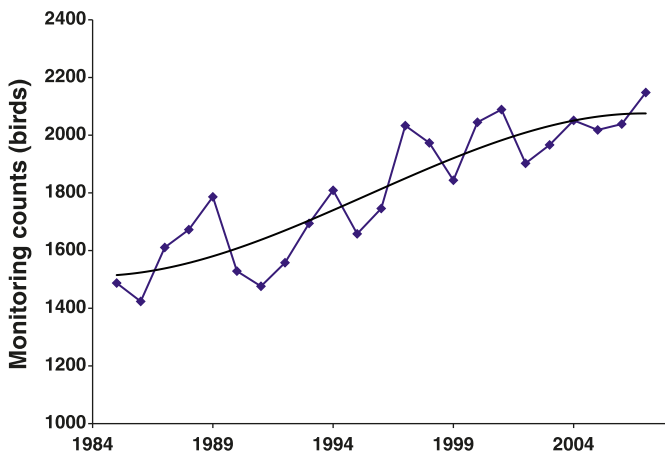


Fig. 8. Trend in Thick-billed Murre population index (counts of fixed study plots) at Coats Island, Nunavut since 1985. Quadratic polynomial fit, $R^2 = 0.79$ (Gaston 2002 and AJG, unpublished data).



The diets of Thick-billed Murre nestlings at Coats and Digges islands have been monitored since the 1980s. In the early years the diets at both colonies were dominated by Arctic cod, but since 1994 the capelin *Mallotus villosus* has made up about half the diet at Coats Island, with cod falling to less than 20% after 2000 (Gaston et al. 2003; Fig. 10). Sandlance also became more common in murre diets during the particularly warm summers of the late 1990s and at that period Razorbills attempted to colonize Coats Island. However, after 2003 sandlance again became rare in murre diets at Coats Island and the Razorbills disappeared (Gaston and Woo 2008). At Digges Island, capelin made up <20% of Thick-billed Murre nestling diets in the 1980s, but comprised 85% in 2004. Arctic cod is an ice-associated fish (Bradstreet and Cross 1982) and these changes may be linked to progressively earlier break-up of sea-ice in Hudson

Fig. 9. Rates of change in Thick-billed Murre population indices (counts at fixed study plots) over the period from 1985 to 2008 expressed as % annual change (AJG, H.G. Gilchrist and MLM, unpublished data).

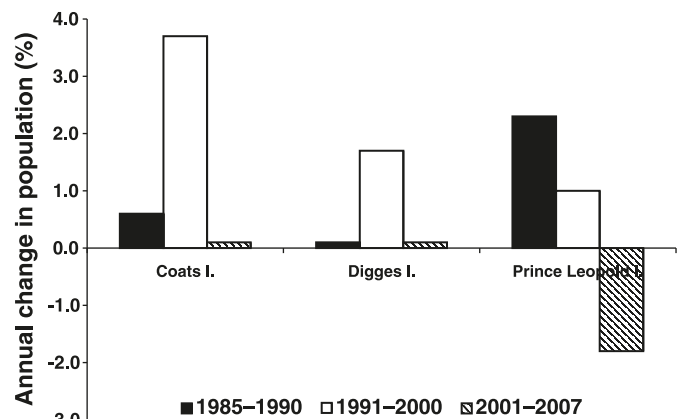
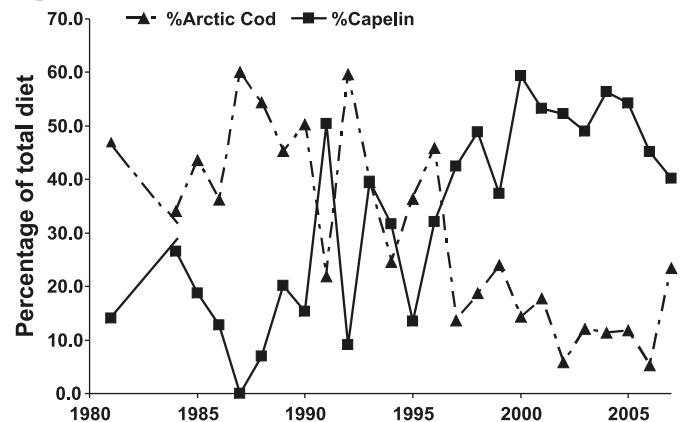


Fig. 10. Proportion of Arctic cod and capelin (% loads delivered) fed to nestling Thick-billed Murres at Coats Island between 1981 and 2007 (no data for 1982 and 1983) (Gaston et al. 2003 and AJG unpublished data).



Bay since the early 1990s (Gagnon and Gough 2005; Stirling and Parkinson 2006).

Zone 5: Southern Labrador, northern Gulf of St. Lawrence and eastern Newfoundland

Seabird trends have been monitored at many colonies in this zone and historical data are available to a much greater extent than in the Arctic zones. The numbers of seabirds in the Migratory Bird Sanctuaries on the Quebec North Shore have been monitored since 1925 and seabird colonies in southeast Newfoundland have been monitored since the 1950s. More recently, significant, if somewhat sporadic, population monitoring has been initiated at Gannet Islands, Labrador, at Magdalen Islands and around Gaspé Peninsula, Quebec. The species most readily monitored, the Northern Gannet has been counted at most Canadian breeding colonies periodically since 1972.

Population trends

North American colonies of the Northern Gannet, spread between Bonaventure and Anticosti islands and Bird Rocks (Gulf of St. Lawrence), to eastern Newfoundland (Funk and Baccalieu islands and Cape St. Mary's), have increased rapidly since the 1950s (Nettleship and Chapdelaine 1988; Chardine 2000; JFR and JWC unpublished data), except for a brief downturn in the Gulf during the early 1970s, probably a result of the effects of organochlorine pesticides on reproduction (Chapdelaine et al. 1987). The two large colonies in the Gulf of St. Lawrence expanded at <2%/year from 1972 to 1984 and then very rapidly from 1984 to 2004 (Bonaventure 4.8%, Bird Rocks 6.5%) with Bird Rocks reaching the exceptional rate of 11.3%/year from 1994 to 1999 (Fig. 11). In Newfoundland, the colony at Funk Island was the most rapidly increasing before 1984 (3.4%), while the colony at Cape St. Mary's expanded rapidly from 1984 to 1999 (6.5%). Although all Newfoundland colonies expanded rapidly from 1994 to 1999, all slowed from 1999 to 2004 with Cape St. Mary's and Funk Island more or less stable (Fig. 11). The rapid expansion of the Bird Rocks colony after 1999 coincided with the withdrawal of lighthouse keepers and their domestic animals from the island that precipitated a rapid expansion of the breeding area from the cliffs surrounding the island to the central plateau (JFR unpublished data). Hence breeding site constraint appears to have been an important factor in determining rate of increase at this colony.

Based on regularly monitoring colonies, patterns of population change for Black-legged Kittiwakes (Fig. 12) and Common Murres (Fig. 13) have been similar throughout the region, with most populations increasing before 1990 and decreasing subsequently, although the very large colony of murres at Funk Island (not included in Fig. 13) has remained stable (see below; Robertson and Elliot 2002; Chardine et al. 2003; Robertson et al. 2004; Rail and Cotter 2007; Cotter and Rail 2007; JFR and GJR unpublished data). Recent trends (since 2000) for smaller colonies of Black-legged Kittiwakes (100s–1000s of pairs) in Newfoundland mainly showed increases (Robertson and Elliot 2002; GJR and P. M. Regular, unpublished data). However, the small offshore colony of Black-legged Kittiwakes on Funk Island decreased from about 800 pairs in the 1980s to less than 200 pairs by 2008

Fig. 11. Trends in Northern Gannets at colonies in the Gulf of St. Lawrence and off eastern Newfoundland since 1972 (source: Nettleship and Chapdelaine 1988, JFR and JWC, unpublished data).

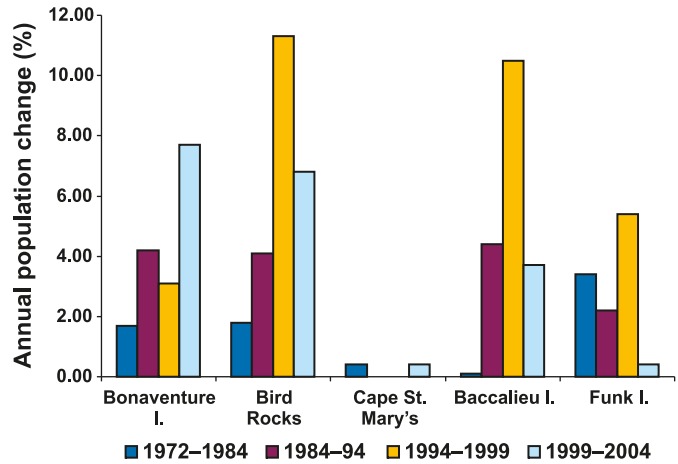


Fig. 12. Changes in numbers of breeding Black-legged Kittiwakes at colonies in Gulf of St. Lawrence and Newfoundland and Labrador (CAFF Seabird Working Group and JFR unpublished data).

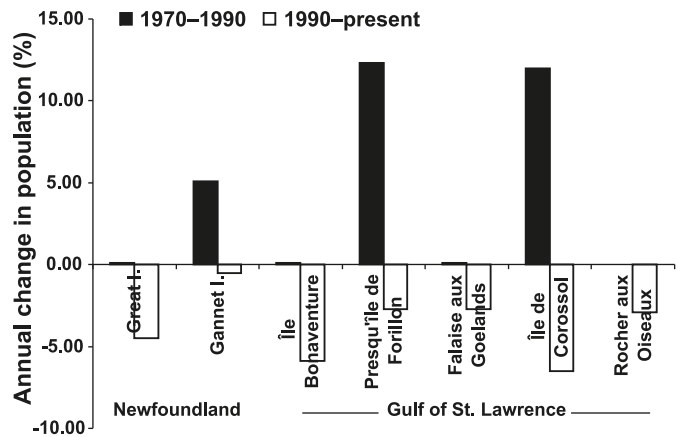
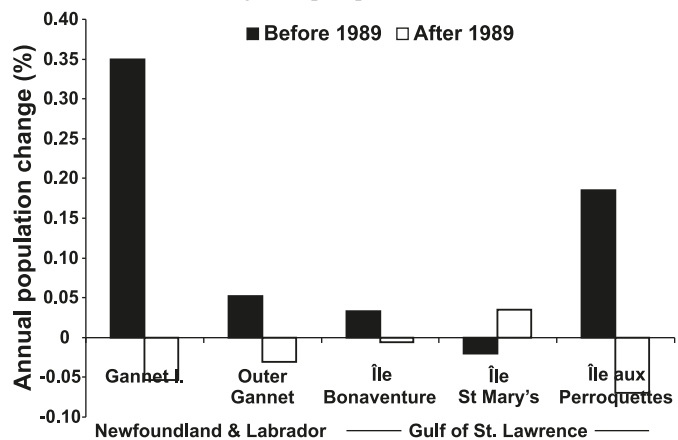


Fig. 13. Changes in numbers of breeding Common Murres at colonies in Gulf of St. Lawrence and Newfoundland and Labrador (CAFF Seabird Working Group unpublished data).



(WAM unpublished data). Small Common Murre colonies in Groswater Bay (central Labrador) increased between 1978 and 2002 (Robertson et al. 2002a), and populations on Gull

and Great Island, Witless Bay (southeastern Newfoundland) also approximately doubled between the 1970s and early 2000s (Robertson et al. 2004).

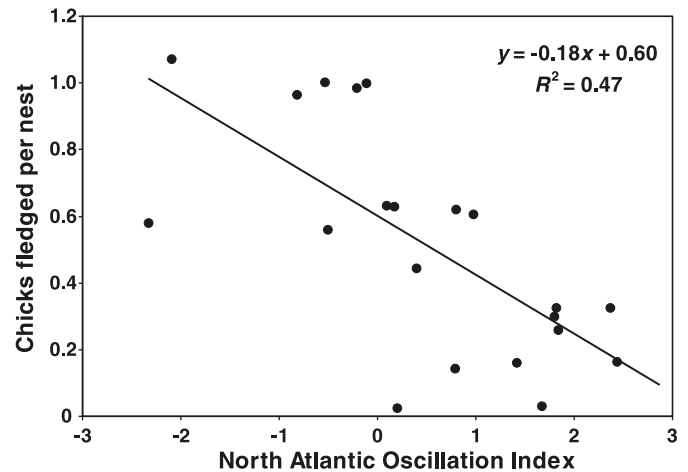
Declines in Black-legged Kittiwake numbers were probably the result of reduced breeding success in the 1990s (see Regehr and Rodway 1999; Massaro et al. 2000 for southeast Newfoundland). Other surface feeders such as Herring Gulls (*Larus argentatus*) also experienced low breeding success at this time (Rodway and Regehr 1999; JWC unpublished data) and were partly responsible for the low breeding success of kittiwakes through high rates of egg and chick predation (Regehr and Montevecchi 1997; Massaro et al. 2000, 2001). This was another result of the cold-water event off eastern Newfoundland in the early 1990s that affected capelin, the major prey of these surface-feeding gulls, in several ways (see above). Ultimately water temperatures in the Northwest Atlantic are related to the state of the North Atlantic Oscillation (NAO). The NAO index experienced an unprecedented increase from the 1960s through 1990s (Visbeck et al. 2001). Breeding success of kittiwakes in Witless Bay colonies is negatively related to the state of the NAO index (Fig. 14).

Other species have shown different patterns of population increase, but lack of census data for the critical period around 1990 prevents assessment of the impacts of that regime shift. Atlantic Puffins in their largest concentration in Witless Bay, Newfoundland showed a small decline between 1979 and 1984 ($-0.8\%/year$) and then a rapid increase from 1984 to 1994 at Great Island ($3.5\%/year$) and between 1984 and 2003 at Gull Island ($8.3\%/year$; Robertson et al. 2004). These are extremely high rates of increase for a species that rears a maximum of one chick annually and does not begin to breed until 4–5 years old, suggesting highly favourable conditions. Methods used in different years may not have been wholly comparable, so that changes from 1979 to 2003 may have been smaller than apparent. However, the area of occupation definitely expanded over that period (Rodway et al. 2003). At Gannet Islands, Labrador, the situation was reversed, with the population increasing from 1978 to 1983 ($4.9\%/year$), then decreasing to 1999 ($-1.1\%/year$; Robertson and Elliot 2002). At nearby Groswater Bay, puffin numbers fell by $-1.2\%/year$ from 1978 to 2002 (Robertson et al. 2002a).

Razorbills at the Gannet Islands showed the opposite pattern to puffins, decreasing from 1978 to 1983 ($-1.3\%/year$), then increasing from 1983 to 1999 ($3.6\%/year$; Robertson and Elliot 2002). The adult survival of Razorbills at this colony is affected by the temperature of Labrador Current waters (survival higher when sea temperature is lower) and this will almost certainly influence population dynamics (Lavers et al. 2008), although a direct link has not been made to date. Razorbills have been steadily increasing throughout the Gulf of St. Lawrence for the last 30 years (Chapdelaine et al. 2001; Coter and Rail 2007; Rail and Coter 2007; JFR unpublished data), as well as in the Bay of Fundy (zone 6, Ronconi and Wong 2003). Overall, this species appears to have been the most successful auk over the past three decades.

Trends at Gannet Islands may have been affected by the arrival of Arctic foxes *Alopex lagopus* in the 1990s (Birkhead and Nettleship 1995) and by a reduction in persecution

Fig. 14. The relationship between Black-legged Kittiwake breeding success at the Witless Bay islands, Newfoundland and the state of the North Atlantic Oscillation. Breeding success is from Maunder and Threlfall (1972), J. Porter (pers. comm.), and JWC and GJR unpublished data from 1990 onwards. Estimates are based on surveys of a large number of nests (1000s) on Gull and Great Islands just before chick fledging took place (GJR and JWC unpublished data). NAO index data is from the Climate Research Unit (CRU), University of East Anglia (<http://www.cru.uea.ac.uk/cru/data/nao.htm>).



by fishermen, which reduced populations in earlier decades (Birkhead 1993). Recovery following persecution before the advent of the *Migratory Birds Conservation Act* (1918) was probably responsible for other increases in seabird populations in this ecozone and in the Gulf of St. Lawrence, Gulf of Maine, and Scotian Shelf during the early part of the 20th century, possibly extending to recent decades. Since 1992 the extent of gill netting off Newfoundland and Labrador and the North Shore of the Gulf of St. Lawrence has been drastically reduced and this must have benefitted all diving birds, especially auks (Piatt and Nettleship 1987; Benjamins et al. 2008). In all, there is little evidence for adverse trends in any auk populations since the 1970s, apart from a downturn in some Common Murre colonies, especially in the Gulf of St. Lawrence after 1990. As this was probably associated with the cold water event of 1990–1991 it seems likely to reverse now that conditions have ameliorated and especially with the reduction in bycatch resulting from the cessation of gill-net fisheries over most of the region. In any case, with only three estimates of population size spanning 34 years at the largest North American colony, at Funk Island, Newfoundland (1972, 396 000 pairs; 2000, 412 000 pairs; 2006, 435 000 pairs; Chardine et al. 2003; Chardine and Robichaud unpublished data) and no estimate of population size since 1973 for the second largest colony at Green Island, Witless Bay (74 000 pairs in 1973), the overall population trend for this species is difficult to assess.

Biological indicators

The relationships between timing of breeding of Common Murres, the timing of inshore arrival of capelin and ocean conditions, show the strong effect of the 1990–1991 cold water perturbation in the Northwest Atlantic. Using data spanning 1980–2006 at Cape St. Mary's, Regular et al.

(2009) showed that both murres and capelin delayed reproduction for two weeks after the 1991 cold water event, but although water temperatures returned to average within a few years, murres and capelin continued to breed later throughout the rest of the 1990s. The best predictor of timing of breeding for murres and of timing of arrival of capelin inshore was the timing of capelin arrival in the previous year, with ocean temperature having a weaker effect (Regular et al. 2009). Although the cues determining these relationships are unknown, this, or similar relationships, apparently led to a delayed response in both birds and fish to conditions in the physical environment, as ocean temperatures returned to pre-perturbation levels much faster than the timing of the animals.

Similar signals of delayed responses of forage fishes to sea surface temperatures were seen in the diets of Northern Gannets at Funk Island (Montevecchi 2007). Gannets are opportunistic, generalist, multi-prey loading predators with broad diet breadths. In the 1980s, warm water species (squid, mackerel *Scomber scombrus*, and Atlantic saury *Scomberesox saurus*) dominated the diet fed to chicks, while cold water species (capelin, herring *Clupea harengus*, sandlance, cod *Gadus morhua*, and salmon *Salmo salar*) dominated from the cold water event in 1990–1991 until 2004 (Fig. 15). The cold SST perturbation that forced a radical shift in pelagic food webs (Montevecchi and Myers 1995, 1996; Montevecchi 2007) returned to pre-perturbation levels by the mid-1990s, but the warm water pelagic fishes did not return to the region until 2005. These types of lags in the biological consequences of physical changes often accompany regime shifts.

In contrast to the gannets, the very large Common Murre population on Funk Island specializes on capelin. Throughout the 1990s, the percentage of gravid capelin, capelin condition, and the energy per capelin delivered to murre chicks decreased (Fig. 16). The decreasing percentage of gravid females was the result of the later spawning of capelin (Carcadden et al. 2002) and a mismatch with the chick-rearing period of the murres (Davoren and Montevecchi 2003). Over this decade, the condition of chicks also decreased significantly. However, this did not affect the size of the breeding population of Common Murres at Funk Island (see above).

At the Gannet Islands, Labrador, seabirds (Common Murres, Atlantic Puffin, Razorbill) fed their chicks significant amounts of capelin in the early 1980s (Birkhead and Nettleship 1985, 1987), but by the late 1990s capelin was largely absent from the diet (Bryant et al. 1999, Baillie and Jones 2004) and has yet to return (Lavers and Jones 2007).

Leach's Storm-Petrel, *Oceanodroma leucorhoa*, which feeds at a lower trophic level than most other seabirds in the Atlantic (Hedd and Montevecchi 2006), had generally stable populations in Newfoundland throughout the 1970s to 2000s (Robertson et al. 2002b, 2006). Large colonies (>100 000s of pairs) that were monitored remained stable, while two smaller colonies, at Middle Lawn and Small islands, declined between the 1980s and 2001, by >10% annually at Small Island. These declines were attributed to the establishment of nearby large gull colonies in the 1970s, which may have made these islands less suitable as breeding sites (Robertson et al. 2006). Diets of storm-petrel nestlings in Newfoundland are dominated by fish (>75%; largely mes-

Fig. 15. Prey landings by Northern Gannets at Funk Island, Newfoundland, 1977–2008. Prey are categorized as either warm (mackerel, Atlantic saury, short-finned squid) or cold water (capelin, herring, Atlantic salmon, sandlance, cod) prey (Montevecchi 2007 and WAM unpublished data).

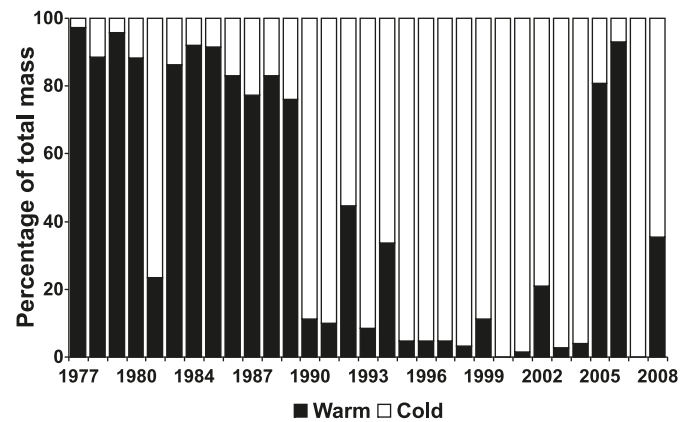
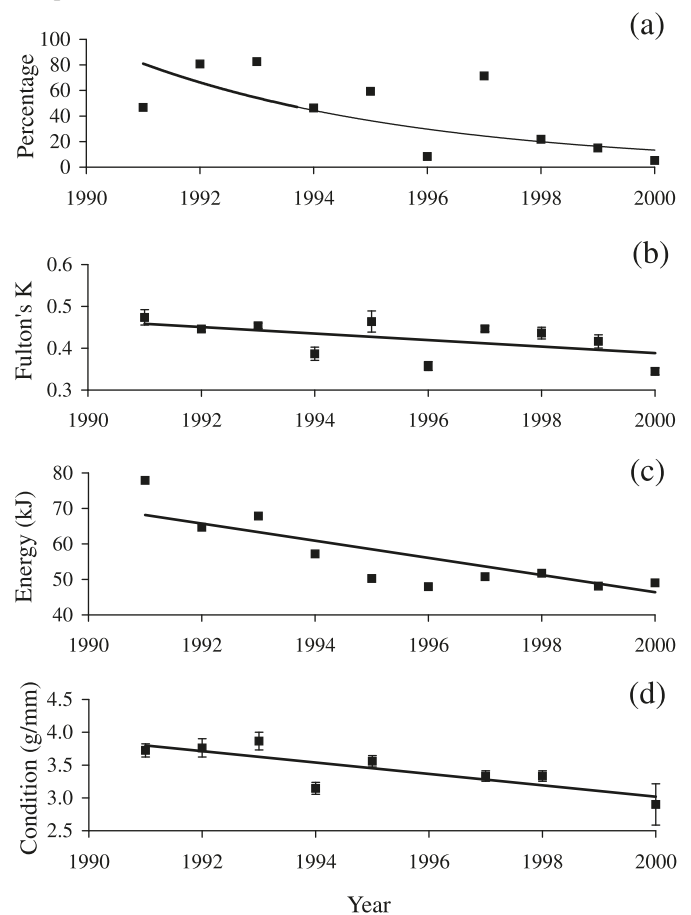


Fig. 16. Annual variation (1991–2000) in (a) the percentage of gravid capelin by number in the diets of common murres, (b) condition (Fulton's K) of female capelin in the diets of murres, (c) mean expected energy delivered per capelin, and (d) condition of murre chicks (mass corrected for wing-length) at Funk Island (adapted from Davoren and Montevecchi 2003).



opelagic lanternfish, Myctophidae) and crustaceans; their general composition was similar in 1987–1988 and 2003–2006 (Hedd et al. 2009). However, crustacean diversity de-

clined: fewer species of hyperiid amphipods were consumed in 2003–2006 and small euphausiids *Thysannoessa* sp. were absent from diets; the later paralleling changes in spring diets of capelin and winter diets of murre species in the region (see below). Nesting chronology on Gull Island, Witless Bay 2003–2005 was similar to that reported for nearby Great Island in 1982 and 1984 (Huntington et al. 1996), suggesting that the timing of breeding has remained relatively constant across this period. Stable trends in Leach's Storm-Petrel populations, diet composition and timing of breeding suggest favourable feeding conditions in recent decades (Hedd et al. 2009).

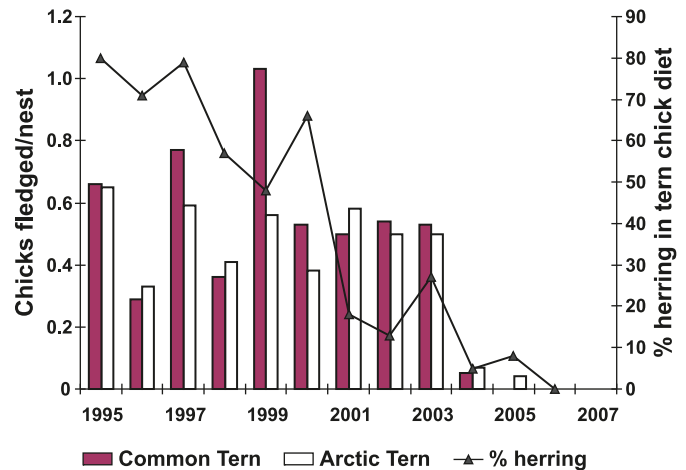
Similar changes in food availability for wintering seabirds have been noted, although data are sparse. In Newfoundland waters, wintering murre diets were largely dominated by capelin in the 1950s (Tuck 1960). In the 1980s, fish (Arctic cod and capelin) were still the most important food item for wintering murre, with euphausiids making up a significant portion of the diet (Elliot et al. 1990). The importance of invertebrates in the diet increased as the winter progressed (Elliot et al. 1990). By the 1990s, fish was present in the diet in similar portions, but capelin and Arctic Cod were both less abundant, and amphipods almost entirely replaced euphausiids as the dominant invertebrate in the diet (Rowe et al. 2000). Also, the decline in the proportion of fish in the diet over the winter season was no longer apparent, indicating that birds were already beginning to rely on invertebrate prey in late fall and early winter (Rowe et al. 2000).

Zone 6: Gulf of Maine and Scotian Shelf (Atlantic Maritime)

In this zone seabird populations are dominated by terns and large gulls, with only small numbers of auks. The most important site for seabird monitoring here is Machias Seal Island, where the Atlantic Cooperative Wildlife Ecology Research Network has conducted studies of terns and auks annually since 1995 (Diamond and Devlin 2003; Clarke et al. 2008). The focus of this work has been on diet and demography, rather than population monitoring. The tern colony has been censused regularly (in alternate years), but there has been only one census each of Razorbill (600 ± 18 pairs in 2000; Grecian 2003) and Atlantic Puffin (2888 ± 44 pairs in 1999; Diamond and Robinson 2000).

Conditions for seabird reproduction at Machias Seal Island were good in the 1990s and early 2000s (>0.5 chicks reared per pair in 7/9 years), but deteriorated sharply after 2003, with few tern chicks (<0.05 chicks/pair) reared thereafter and few breeding attempts by terns in 2006, 2007, and 2008 (all unsuccessful). Numbers of breeding terns peaked in 2002 with over 3000 pairs, of which two-thirds were Arctic and the rest Common Terns (*Sterna hirundo*, Diamond 2007). This was the largest known Arctic Tern colony in North America, and the largest tern colony in the Gulf of Maine. Birds banded as breeders on Machias Seal Island are known to have dispersed to other colonies in the Gulf of Maine (Devlin et al. 2008). The continuous occupation of this colony since at least the 1870s (MacKinnon and Smith 1985), interrupted only once (in 1944) by colony abandonment, emphasises the significance of its recent desertion and raises the question of just what it signifies in terms of changes in the ocean ecosystem. The desertion of the tern

Fig. 17. Changes in reproductive success of Common and Arctic Terns at Machias Seal Island during 1994–2007 and proportion (by number of items) of Common Tern nestling diets made up by herring (Clarke et al. 2008).



colony was associated with a change in nestling diets from herring to other fish or crustacea (Fig. 17), exacerbated by increased predation by Herring and Great Black-backed (*L. marinus*) Gulls. Prior to 2001, the primary food for chicks of Razorbills, Atlantic Puffins and the two tern species was < 1 year-old Atlantic Herring (*Clupea harengus*); in terns and Atlantic Puffins these were replaced in 2001 by juvenile sand lance (*Ammodytes* sp.), and thereafter by euphausiid crustacea (*Meganactiphanes norvegicus*) and larval fish. Herring continued as a major diet item in Razorbills, though still declining steeply from pre-2001 levels. The drop in tern productivity preceded abandonment of the colony by two years. It began with euphausiids and larval fish becoming dominant in chick diets. In Razorbills and Atlantic Puffins, there was a two-year lag between the switch to euphausiids and fish larvae, and a reduction in breeding success (Clarke et al. 2008). Predation by gulls — primarily on eggs and chicks, initially on terns but latterly on auks — increased over the same period, and was the proximate cause of the abandonment of the tern colony in 2006. The increase in gull predation may have been related to change in the food web, with terns in poor condition being less likely to drive gulls away (AWD unpublished data).

Common Murres colonized Machias Seal Island in 2002 after spending four years prospecting and reached ~ 150 pairs before declining in response to gull predation of eggs laid in exposed sites (AWD unpublished data). Elsewhere in the Bay of Fundy, several changes in distribution probably still reflect a long, lagged response to protective legislation in the early 1900s. Black-legged Kittiwakes had not been recorded breeding in the Bay since the early 1800s, but a small colony was found on South Wolf Island in 1992 (Kehoe 1994) and in 1998 >40 pairs were found on Whitehorse Island, 12 km NW of South Wolf (Kehoe and Diamond 2001). Whitehorse Island was also the site of an unsuccessful breeding attempt in 1999 by several pairs of Northern Gannets, which had also been absent from the Bay since the 1880s (Corrigan and Diamond 2001).

Great Black-backed and Herring Gulls, both large, predatory and piscivorous species, increased rapidly in eastern

North America after 1950, being regarded as a pest in many areas (Kadlec and Drury 1968). Increases continued in most areas up to the 1980s, following which many populations declined (Boyne and Beukens 2004; Boyne and McKnight 2005). However, monitoring, outside of the Migratory Bird Sanctuaries of the Quebec North Shore, has been very sparse, so the cause of the change in population trend cannot be identified. On the North Shore it seems to have coincided with the 1990 cold water event and the consequent changes in fisheries (Chapdelaine and Rail 1997). Both of these species make extensive use of fish offal from fishing boats and processing plants and the reduction of this food source may have accounted for the changes. Ring-billed Gulls (*Larus delawarensis*) have increased rapidly in the Gulf of St. Lawrence and numbers around the coast of Newfoundland probably have increased (Boyne and McKnight 2005; Boyne et al. 2006; CWS unpublished data). This species makes substantial use of land and freshwater habitats and hence its recent spread in zones 5 and 6 may have been little affected by marine conditions.

Tern numbers in Nova Scotia, Prince Edward Island, and New Brunswick showed no consistent trend since the 1970s. Their fluctuations may have been affected by increased disturbance of the coastal zone (e.g., wind-turbine placements) and, in the period up to the mid-1980s, the increasing numbers of large gulls (Boyne et al. 2001; Boyne and Hudson 2002). However, a decline in the number of breeding colonies over the last 30 years is a cause for concern (Boyne and McKnight 2005; Boyne et al. 2006). Terns switch unpredictably among potential breeding sites, making counting them a challenge. It is hard to know how much their population fluctuations are affected by the marine environment, although the recent desertion of Machias Seal Island probably has to do with negative changes to marine food webs, as well as increased predation by large gulls.

Conclusions

Our ability to track environmental change through changes in the biology of marine birds is inevitably constrained, both by the attributes of individual species and by our ability to develop cost-effective methods to study them. In general, open nesters (e.g., gannets, murre, gulls) have been more accurately and effectively monitored than those nesting in burrows or crevices (e.g., storm-petrels, puffins). Integrated programmes that study several species of varying ecology at the same locality are likely to be more useful than single-species studies. Given that many seabird colonies are expensive to access, multi-species studies are likely to be more cost-effective as well. Studies of species for which adult or nestling diets can be readily sampled without killing birds have proven especially valuable.

A picture of large-scale trends in Canadian marine bird populations is beginning to emerge after several decades of monitoring and research. Along Pacific, Arctic, and Atlantic coasts, marine birds have exhibited significant short- and long-term responses to the condition of the marine ecosystem in the oceanic zone of their colonies. Generally, because of coarse sampling programmes, the effects of physical events on population trends were not detected for several years, in some cases decades. However, annual population

monitoring at Coats Island suggests that even numbers of breeders can react quickly to environmental change, with a sharp drop in numbers coinciding with the 1990 cold water event off Eastern Canada (Fig. 7). As predicted (Gill and Hatch 2002; Gill et al. 2002), nestling diets and growth rates reacted to environmental changes very rapidly (Parsons et al. 2008). This was exemplified by diet change in the Funk Island Northern Gannet population in 1990 (Fig. 15), a signal that was detected at virtually the same time as physical indices changed. Indicators including diet and nestling growth are currently being monitored annually at sites in zones 1 (Triangle Island), 4 (Coats Island), 5 (Funk Island), and 6 (Machias Seal Island). The continuation and expansion of this network to the other zones is clearly desirable.

In the Pacific, processes associated with the state of the California Current system have affected the very large populations of auks breeding at Triangle Island. Conditions there have been more often negative than positive since the 1970s, leading to downward trends in populations of Cassin's Auklets, Rhinoceros Auklets, and Common Murres. Some of the negative effects may have been created by a mismatch between the timing of breeding by the birds and the peak of food availability: this has been confirmed for Cassin's Auklets (Hipfner 2008) and may be true for other species.

Conditions in areas of the Pacific Ocean north of the upwelling influence associated with California Current zone, principally the Hecate Strait region and west coast of Haida Gwaii, have been better, with auk populations generally increasing. A signal, in the form of late and less successful breeding by auklets and murrelets, appeared during the strong El Niño – Southern Oscillation event of 1997–1998 (Gaston and Smith 2001), but otherwise conditions in this zone appear to be largely uncoupled from those farther south.

On the Atlantic seaboard, in the Gulf of St. Lawrence, on the Scotian Shelf and around Newfoundland and Labrador, the sharp discontinuity in oceanography and food webs that occurred in the early 1990s caused some marine bird populations, especially gulls, to shift from positive to negative trends. However, Northern Gannets and Razorbills increased more or less continuously from the 1970s onward, as have most auk populations within the Gulf of St. Lawrence and Atlantic Puffins in southeast Newfoundland. The groundfish moratorium off eastern Newfoundland caused the closure of gill-net fisheries that were drowning many auks. Removal of this source of mortality has had positive consequences for some populations of diving birds (Benjamins et al. 2008). Conversely, terns generally were stable or decreased throughout the period from the 1970s onwards in these zones, possibly as a result of human influences on their terrestrial breeding habitat. Decreases in large gulls and Black-legged Kittiwakes may have related to the reduction in in-shore fisheries activity (which provided fish offal and discards) following the groundfish moratorium of 1992 and to the changes in capelin size, distribution, and timing that occurred at that time (Regehr and Montevecchi 1997; Regehr and Rodway 1999; Massaro et al. 2000; Carscadden et al. 2001; Robertson et al. 2001).

Positive trends in seabird populations in Atlantic Canada prior to 1990 may have reflected continuing recovery from

egging and plumage harvesting prevalent before the institution of the *Migratory Bird Conservation Act* (1918) in the early twentieth century, or in Newfoundland, after confederation with Canada in 1949. Some harvesting activities continued to affect seabirds on the North Shore of the Gulf of St. Lawrence as late as the 1960s and 1970s (Blanchard 1984) and may continue still in some isolated parts of Atlantic Canada.

Seabird populations breeding in the two Eastern Arctic zones, Arctic Archipelago and Hudson Bay and Foxe Basin, with the exception of Ivory Gulls throughout their range and of Black-legged Kittiwakes at Prince Leopold Island, have shown mostly slow changes in population (rates of change $< \pm 2\%$ /year). Thick-billed Murres, the only species for which detailed information is available over several decades, have shown congruent population trends for colonies in Hudson Bay (Digges and Coats islands) and the High Arctic (Prince Leopold Island), suggesting that the dynamics are determined by events on the common wintering areas in the Northwest Atlantic (Gaston 2002, 2003). This may be true for other species as well; for example, Razorbills from throughout the breeding range (Labrador, North Shore, and Bay of Fundy) spend at least part of the winter in the region around Grand Manan Island in the Bay of Fundy (Huettmann et al. 2005; T.C. Clarke and AWD unpublished data). Seabird monitoring in these and other zones should be analysed in conjunction with trends in ocean conditions in the Northwest Atlantic as a whole.

Changes in diet and nestling growth at Coats and Digges islands are probably related to reduction in spring and summer sea-ice cover in Hudson Bay (Gaston et al. 2005b), and perhaps mediated by a mismatch between timing of ice break-up and timing of egg-laying (Gaston et al. 2009a). The interaction between timing of ice break-up and nestling growth and reproductive success of several species at Prince Leopold Island suggests that earlier ice break-up, as a result of warmer spring weather, could benefit populations breeding there (Gaston et al. 2005b). However, recent population trends at that site differ among species and, as noted above, are more likely to be accounted for by conditions outside the breeding season. No changes in diet have yet been noted at Prince Leopold Island, suggesting that changes seen in northern Hudson Bay have not yet extended north of the High Arctic boundary.

The generalisations that we have made depend somewhat on the assumption that most populations are driven predominantly by survival and internal recruitment. The extent to which redistribution of breeding birds may affect the population dynamics of individual colonies is largely unknown, as few seabird studies have involved multiple colonies. Terns and Cormorant colonies may appear and disappear from year to year and it seems certain that such changes involve the relocation of breeding birds among sites. Other seabirds relocate mainly during the pre-breeding phase, when some species show substantial natal dispersal (e.g., gulls, Gaston et al. 2009b). However, most auks except Ancient Murrelets appear to recruit mainly to their natal colonies (Gaston and Jones 1998). The degree to which redistribution of populations affects the interpretation of population monitoring results is an important topic for further research.

To date, seabird monitoring in Canada has revealed striking dynamism within populations: among species monitored for more than 15 years, Northern Gannet, Glaucous Gull, Herring Gull, Ivory Gull, Black-legged Kittiwake, Arctic Tern, Common Murre, Cassin's Auklet, and Atlantic Puffin have all exhibited $\pm 7\%$ annual rates of population change, equivalent to doubling or halving in a decade in at least one region. Moreover, there are clear demarcations in population trends and biology between zones, with auks increasing in Haida Gwaii (zone 2), while decreasing, at least at Triangle island, in zone 1 and Black-legged Kittiwakes increasing in the Arctic (zone 3) while decreasing in Atlantic Canada (zone 5). However, all species showed substantial concordance within regions. This finding emphasizes the need for distributed monitoring that takes account of marine boundaries. At the same time, it suggests that the monitoring of selected colonies, provided they are not subject to unusual point-source perturbations, can give an adequate signal of regional trends. This finding supports the concept that, given limited resources, a small network of intensively monitored sites, may be more useful than a larger network of intermittently monitored sites.

Our oceans are currently affected by many human activities, including climate change, fishing, resource extraction, transportation, particulate and chemical pollution (e.g., Coe and Rogers 1997; Melvin and Parrish 2001; Schreiber and Burger 2002; Stenseth et al. 2004; ACIA 2005). Any of these factors, alone or in concert with other changes, has the potential to markedly alter marine ecosystems. We can learn much about ecosystem condition by studying seabirds (reviewed in Boyd et al. 2006). In Canada, for example, diet monitoring has reflected striking changes in marine food webs, one of which (increase in capelin in northern Hudson Bay) was not detected by any other means. This provides evidence that seabird monitoring can contribute to a general understanding of changes in marine ecosystems. At the same time, we are beginning to appreciate the role of physical factors and other drivers of primary productivity in the dynamics of marine bird populations. If monitoring efforts can be intensified, better monitoring of population changes, combined with more extensive monitoring of diets could provide more sensitive and timely information on future ecosystem changes.

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