

Changes in oceanographic conditions off northern British Columbia (1983–1999) and the reproduction of a marine bird, the Ancient Murrelet (*Synthliboramphus antiquus*)

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Abstract: We examined variation in breeding-biology parameters for Ancient Murrelets (*Synthliboramphus antiquus*), marine birds breeding in central Hecate Strait, British Columbia, over the period 1983–1999. Interannual changes were compared with physical oceanographic data (sea-surface temperatures (SSTs) and Southern Oscillation (SO) indices) for surrounding waters. No secular change in oceanographic data for Hecate Strait was detectable for the period considered, which embraced two major (1982–1983, 1997–1998) and three minor El Niño – Southern Oscillation (ENSO) events. SSTs were strongly related to the SO index for the area considered. Breeding-biology data were not available for the 1982–1983 ENSO. The 1997–1998 ENSO had a strong effect on breeding success, reducing the number of chicks per pair from >1.4 to below 1; most of this effect was caused by desertions before incubation began. We found a positive correlation between May SST and the slope of the regression of chick mass at colony departure on a particular date for a given year. This effect may have resulted from the failure of young or otherwise less competent birds to rear young in years of high SSTs. Both the median date of colony departure and chick mass at departure declined over the period of the study, although neither effect was related to changes in the oceanographic variables considered in this study. These trends may relate to longer term changes in oceanographic conditions in the North Pacific Ocean. If they continue, the recent trend towards lower chick masses at colony departure may have adverse effects on recruitment and eventually on Ancient Murrelet populations.

Résumé : Nous avons étudié la variation des paramètres de la biologie de la reproduction de 1983 à 1999 chez le Guillemot à cou blanc (*Synthliboramphus antiquus*), un oiseau marin qui se reproduit dans la région centrale du détroit d'Hécate, en Colombie-Britannique. Les changements inter-annuels ont été comparés aux données océanographiques, températures de surface de la mer (SSTs) et indices d'oscillation australe (SO) des eaux avoisinantes. Aucun changement séculaire dans les données océanographiques du détroit d'Hécate n'a pu être décelé au cours de la période étudiée, qui a subi deux événements majeurs (1982–1983, 1997–1998) et trois événements mineurs El Niño – oscillation australe (ENSO). Les températures de surface de la mer (SSTs) étaient fortement reliées à l'indice SO pour la région étudiée. Nous n'avons pas de données sur la reproduction au cours de l'ENSO de 1982–1983. L'ENSO de 1997–1998 a eu un effet considérable sur le succès de la reproduction : le nombre de poussins est passé de >1,4 à moins de 1, surtout à cause d'abandons avant le début de l'incubation. Il existe une corrélation positive entre la température SST de mai et la pente de la régression de la masse des poussins au départ de la colonie en fonction de la date pour une année donnée. Il se peut que cet effet soit le résultat de l'échec des tentatives de reproduction de jeunes oiseaux ou d'oiseaux moins compétents les années de SST élevée. La date médiane du départ de la colonie et la masse des poussins au moment du départ ont diminué pendant la durée de l'étude, bien que ni l'un ni l'autre de ces effets n'ait pu être relié à des changements dans les variables océanographiques prises en compte. Ces tendances sont peut-être associées à des changements à long terme des conditions océanographiques dans le Pacifique-Nord. Si elle continue, la tendance récente à la diminution de la masse des poussins au départ de la colonie pourrait avoir des effets nocifs sur le recrutement et éventuellement sur les populations de Guillemots à cou blanc.

[Traduit par la Rédaction]

Introduction

Colonial seabirds can be useful indicators of changes in marine ecosystems. The aggregation of large numbers of birds at predictable localities during the breeding season means

that data can be obtained which integrate oceanic effects taking place over the area within foraging range of the colony (Boersma 1978; Cairns 1992; Montevecchi 1993; Montevecchi and Myers 1996). Foraging ranges of auks commonly reach 100 km (Gaston and Jones 1998). Seabirds feeding on com-

Received February 6, 2001. Accepted August 14, 2001. Published on the NRC Research Press Web site at <http://cjz.nrc.ca> on September 21, 2001.

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mercially fished species are sometimes sensitive to changes in local fish stocks (Uttley et al. 1989; Hamer et al. 1993; Bertram and Kaiser 1993; Montevecchi and Myers 1997). Birds that prey on organisms not directly affected by commercial fisheries may be more sensitive to changes in productivity related to fluctuations in oceanographic conditions (Ainley et al. 1994; Ainley et al. 1996a).

Trends in zooplankton stocks (Mackas et al. 1998) and seabird populations (Bertram et al. 2000) off the coast of British Columbia suggest that decadal-scale changes may have taken place in the area's marine ecosystems, as well as elsewhere in the northeast Pacific Ocean during the past several decades (Ainley et al. 1994, 1996b; Roemmich and McGowan 1995).

In the last 20 years, five El Niño – Southern Oscillation (ENSO) events have affected waters off British Columbia: two strong ones (1982–1983 and 1997–1998) and three weaker ones (1986–1987, 1991–1992, and 1994) (Freeland 1998). Generally, strong ENSO events occur only once every decade, with intervals of sometimes up to 20 years (Duffy 1993). Hence, long-term studies are needed to assess the effects of such oceanographic fluctuations on seabirds and other wildlife. Major ENSOs have had severe effects on many marine birds breeding at the Farallon Islands, California, in the centre of the California Current upwelling zone (Ainley and Boekelheide 1990). Only a few studies have examined the effects of ENSO events on marine birds in British Columbia or elsewhere in the northeast Pacific Ocean (Wilson 1991; Piatt and Van Pelt 1997; Burger et al. 1998; Morgan 1999). No systematic comparative data dealing with the effects of interannual variation in oceanographic conditions on the biology of a marine bird in British Columbia have been available hitherto.

To assess the impact of oceanographic changes on marine birds in northern British Columbia waters, we summarize results from a long-term study of Ancient Murrelets (*Synthliboramphus antiquus*) in Haida Gwaii (Queen Charlotte Islands) during 1984–1999 that provide an up to 15-year dataset on various aspects of Ancient Murrelet breeding biology. We also compare changes in annual productivity with changes in indices of physical oceanographic conditions over the same period to evaluate the effects of ENSO events on seabirds in the Hecate Strait region and determine how much of the interannual variation in breeding biology may be explained by such changes.

Ancient Murrelets are colonial burrow nesters. Two eggs are laid each year; the chicks leave the colony with the parents 1–3 days after hatching and return to breed at 2–3 years old (Sealy 1975; Gaston 1992). Adults may live as long as 17 years (A.J.G., unpublished data). They feed primarily on larger zooplankton (*Euphausia pacifica* and *Thysanoessa spinifera*), as well as immature Pacific sand lance (*Ammodytes hexapterus*), capelin (*Mallotus villosus*), and walleye pollock (*Theragra chalcogramma*) (Sealy 1975; DeGange and Sanger 1986; Vermeer et al. 1987; Perry and Waddell 1997). Birds from the study colonies are believed to feed principally in southern Hecate Strait while breeding (Gaston 1992).

Methods

Information on sea-surface temperatures (SSTs) and Southern

Oscillation (SO) indices reported here were obtained from the Institute of Ocean Sciences Lightstation Data Web site (<http://www.ios.bc.ca/ios/osap/data/lighthouse/bcsop.htm>). For comparison with seabird breeding data, we used the mean of SSTs reported for the four stations nearest to Haida Gwaii: Langara Island, Bonilla Island, McInnes Point, and Kains Island (Fig. 1). SSTs are expressed as the mean of deviations from the 40-year (1960–1999) average for March (just prior to egg laying) and May (peak departure period for chicks). Annual SO indices used were the means of monthly values for January–March and the mean change in SO indices between the preceding September and March of the year considered. Although observations of seabirds began only in 1984, analyses of oceanographic data were based on the period 1983–1999 in order to include two major ENSO events.

Biological parameters for Ancient Murrelets were measured at two breeding colonies in Laskeek Bay in the central part of Hecate Strait: Reef Island (1984–1989, 1995, 1997, and 1999) and East Limestone Island (1990–1999). We measured the following aspects of Ancient Murrelet breeding biology: reproductive success, egg size, adult body mass at hatching, median date of chick departures, and mean chick mass at departure. Timing of breeding was similar at the two colonies in overlapping years (Gaston and Harfenist 1998) and no significant difference was found between colonies for any of the parameters measured in this study. Consequently, we treated data from either colony as representative of conditions in the area in a given year, combining data for the two colonies when available in the same year.

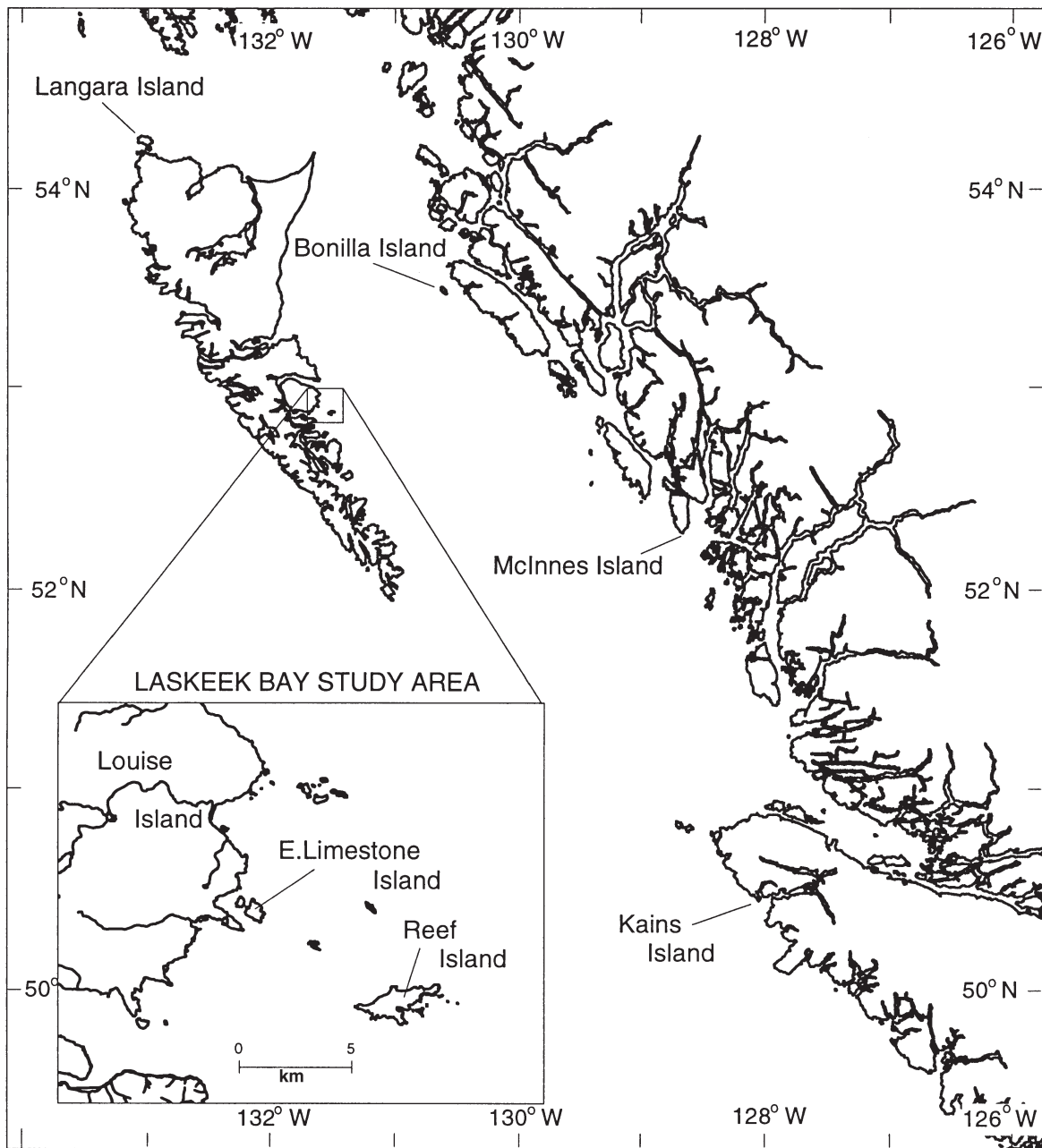
On both islands, from early April to mid-May study burrows were numbered and twigs were placed in burrow entrances so that they had to be moved by birds entering. Displacements of twigs, indicating burrow visits, were noted daily. If burrows had been entered, they were checked for the presence of the first egg. When found, the egg was measured (length and breadth \pm 0.1 mm) and a temperature probe was installed to monitor subsequent incubation without disturbing the breeders (Gaston 1990). After 30 days the contents of the burrows were examined and the 2 chicks and one or both of the parents were banded and weighed. Adults were weighed with a 300- or 500-g Pesola spring balance (\pm 1 g) and chicks were weighed with a 50-g Pesola spring balance (\pm 0.5 g). Egg size was estimated using an index of egg volume (length \times breadth²). Reproductive success data (number of chicks fledged per nesting pair) were collected on Reef Island in 1987–1989 and on East Limestone Island in 1991–1999 (12 colony-years). The mean egg-volume index for first eggs and mean adult mass were estimated for 15 years (1984–1989 and 1991–1999).

To estimate median chick-departure dates and chick mass at departure, plastic fences were used to intercept chicks departing from the colonies and guide them to catching sites near the shore (Gaston et al. 1988). Fences were placed in exactly the same location each year and chick captures were monitored from 7 May until the first night when no chicks were caught. Chicks were banded and weighed as they arrived at the catching site and released to the sea within 5 min. Data were analysed using captures between 23:00 and 02:30 each night, the period when >90% of chicks departed (Gaston 1992).

Both adult and chick masses usually decline with date in a given year (Gaston 1992). Hence, we analysed the trends of mass on a particular date for each year, using the slope of the relationships (regression coefficients) as a measure of the change in mass of breeders and departing chicks over the season.

We compared interannual variation in the timing of chick departures, breeding success, chick mass at departure, egg size, and trends in adult and chick masses on a particular date with changes in the SO index and mean March and May SSTs. All statistics were computed using the multiple-regression module of Statistica software (Statsoft 1995).

Fig. 1. Map showing the locations of sea-surface temperature (SST) sampling sites (light stations) and Ancient Murrelet (*Synthliboramphus antiquus*) study colonies (inset).



Results

Time trends

Median departure dates for chicks became earlier over the period of the study ($r_{[16]} = -0.628$, $P = 0.009$; Fig. 2) and the mean mass of chicks at departure from the colony declined ($r_{[16]} = -0.685$, $P = 0.005$; Fig. 3). There was no evidence that either relationship was affected by the occurrence of ENSO events (years marked with arrows in Figs. 2 and 3). We found no correlation between chick mass and median departure date ($r_{[15]} = 0.08$, $P = 0.78$). Breeding success and adult mass did not change over time ($r_{[11]} = -0.328$, $P = 0.324$, and $r_{[16]} = 0.382$, $P = 0.160$, respectively). No trends across years were detectable in the regressions of chick mass

or adult mass on date within a given year ($r_{[15]} = 0.388$, $P = 0.153$, and $r_{[15]} = 0.102$, $P = 0.716$, respectively).

Correlation with SST and SO index

There was substantial interannual variation in March SST for the region and values were strongly correlated with SO indices, with warm water prevailing in years of high SO indices (Fig. 4). However, we found no overall secular trend in SSTs over the period 1983–1999.

Breeding success was negatively correlated with March SST and change in the SO index ($r_{[11]} = -0.640$, $P = 0.034$, and $r_{[11]} = -0.707$, $P = 0.015$, respectively; Fig. 5). In 1998, following the strongest ENSO of the period considered, Ancient Murrelets reared <1 chick/pair compared with an

Fig. 2. Median dates of departure of Ancient Murrelet chicks reared at East Limestone and Reef islands during 1985–1999. Arrows indicate years of ENSO events.

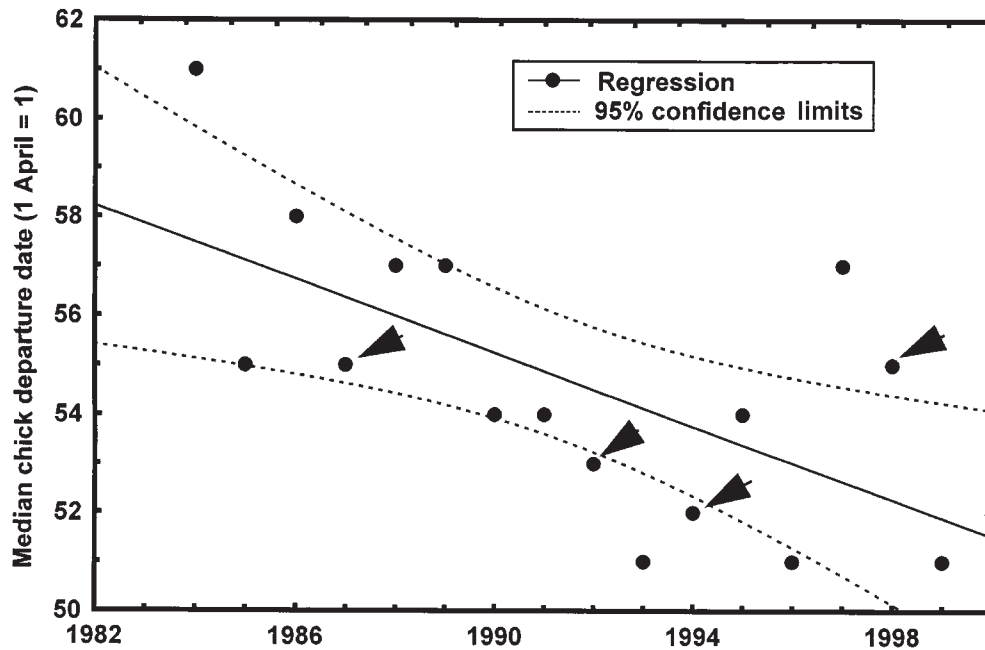
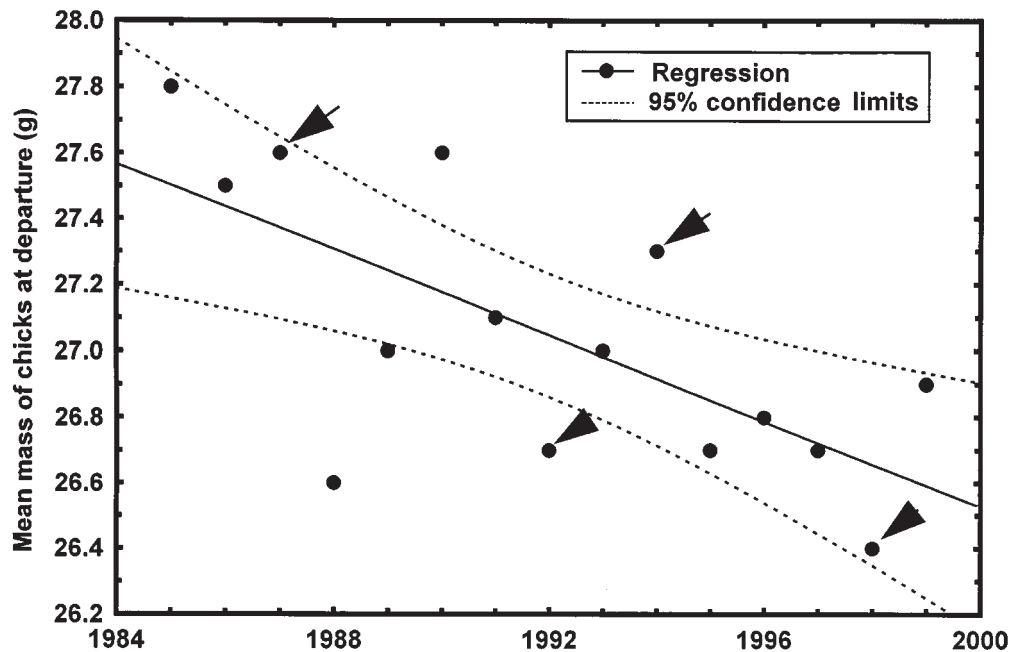


Fig. 3. Mean masses at departure of Ancient Murrelet chicks reared at East Limestone and Reef islands during 1985–1999. Arrows indicate years of ENSO events.



average of >1.4 chicks/pair in other years. When 1998 was excluded there was no significant relationship, suggesting that the murrelets can compensate for oceanographic changes within the normal range of SSTs. Neither March SST, May SST, nor the SO index showed a correlation with adult mass or egg-volume index (all $P > 0.3$).

The mean mass of chicks at departure was negatively correlated with May SST ($r_{[15]} = -0.592$, $P = 0.020$), but in a multiple-regression analysis with year and May SST as

independent variables, only year was significantly correlated with chick mass. The seasonal trend in chick mass (slope of regression of chick mass at departure on date) was positively correlated with May SST ($r_{[15]} = 0.619$, $P = 0.014$; Fig. 6). Hence, late-departing chicks were lighter relative to early-departing chicks in years when SST was low than in years when it was high. In 3 out of the 4 ENSO years the regression coefficient for chick mass on date fell below the 95% confidence limits on the regression of annual trend on SST.

Fig. 4. Southern Oscillation (SO) index deviations from the long-term mean (1960–1999) for November–March (mean winter) and March, and SST deviations from long-term means for March.

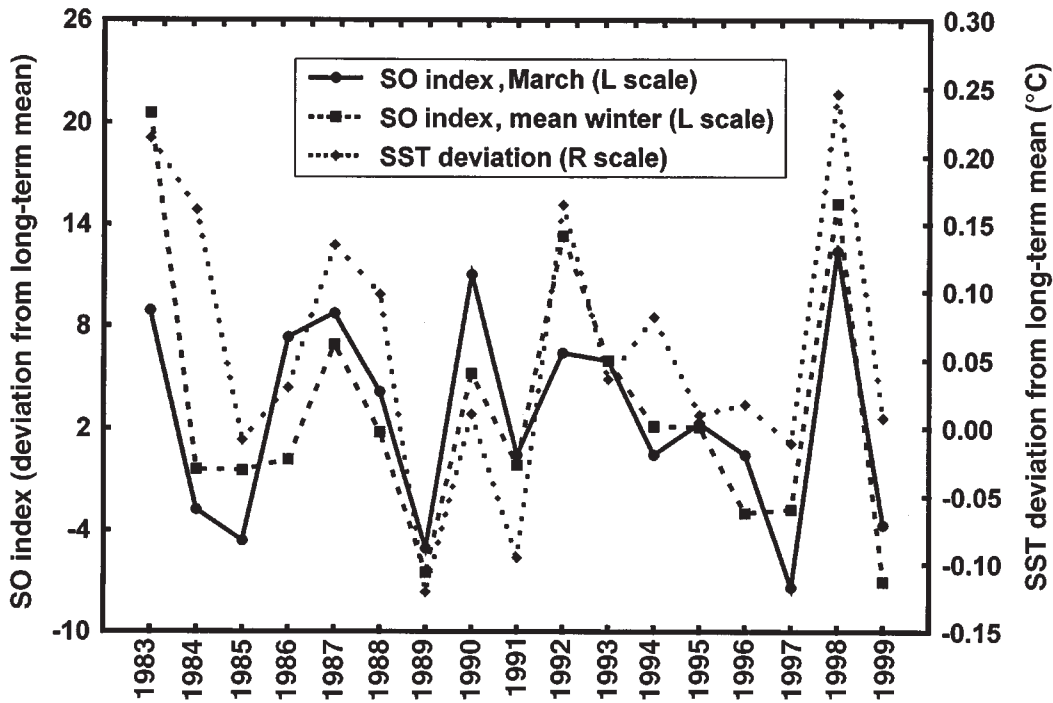
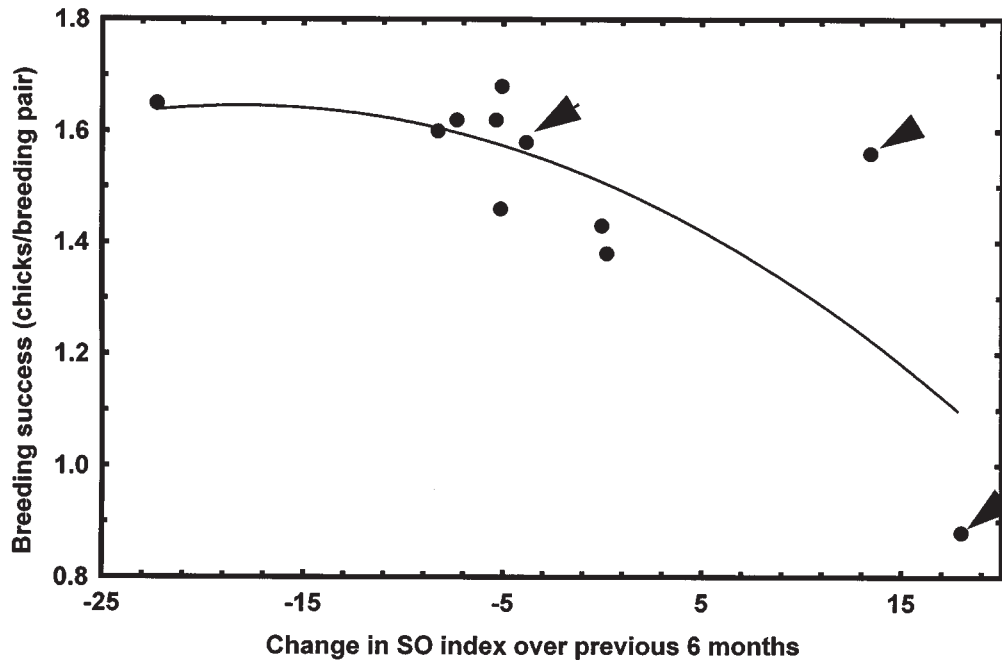


Fig. 5. Breeding success of Ancient Murrelet pairs at East Limestone and Reef islands during 1988–1999 in relation to the change in the SO index over the previous 6 months (September–March). The fitted curve is smoothed negative exponential.



In a multiple-regression analysis using year, SO index, and May SST, only May SST had a significant effect.

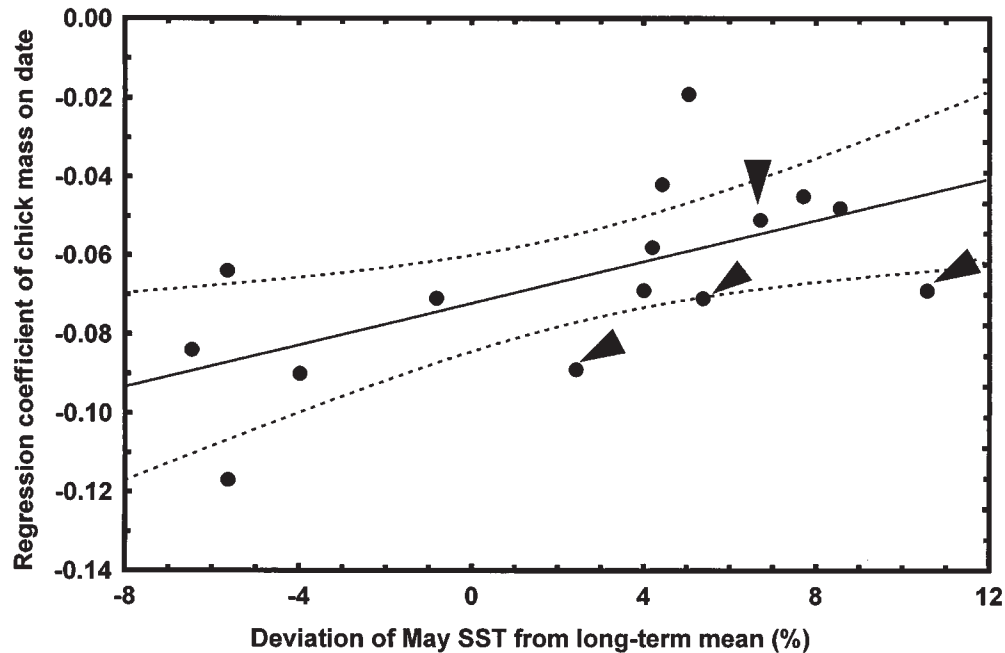
Discussion

SSTs in the Haida Gwaii region closely followed changes in the SO index for the period 1983–1999. There was no indication that the temperature anomalies coincident with ENSO

events at the light stations considered were affected by the oceanographic domain in which they occurred (Ware and McFarlane 1989; Francis et al. 1998). Nor was there any indication of secular change in SST during the period considered.

Among Ancient Murrelet breeding biology parameters measured, only breeding success (mean number of chicks departing per breeding pair) and the regression of chick departure

Fig. 6. Regression coefficient for chick mass at departure on a particular date in relation to mean SST in May of the departure year.



mass on date showed any correlation with changes in local SSTs or in the SO index. The mean mass of chicks at departure was correlated with May SST, but this correlation was not significant when year and SST were combined in a multiple-regression analysis.

The correlation between SST and the breeding success of Ancient Murrelets was most strongly affected by events in 1998, when the highest SSTs of the period coincided with an unusually high rate of nest failure. Around Haida Gwaii and Vancouver Island, warm-water anomalies persisted from the winter of 1997 to the spring of 1998 (Freeland 1998), both prior to and during the 1998 breeding season for Ancient Murrelets. Elsewhere in British Columbia, other seabirds experienced reduced reproductive success or declines in numbers: Cassin's Auklets (*Ptychoramphus aleuticus*) on Triangle Island experienced poor reproductive success in 1998 (D.F. Bertram, personal communication), and in the Carmanah-Walbran valleys on western Vancouver Island, reduced numbers of Marbled Murrelets (*Brachyramphus marmoratus*) were active around nest sites (A.E. Burger, personal communication). However, Cassin's Auklets breeding at Frederick Island on the west coast of Haida Gwaii did not experience reduced breeding success (A. Harfenist, personal communication). This colony was apparently less affected than others by the ENSO of 1997–1998.

Previous strong ENSO events have disrupted breeding for many species of seabirds in California (Ainley and Boekelheide 1990). In Oregon and Washington, ENSO events caused sharp declines in numbers of two cormorant species (*Phalacrocorax penicillatus* and *Phalacrocorax auritus*), and were partly responsible for colony abandonment by breeding Common Murres (*Uria aalge*) (Hodder and Graybill 1985; Wilson 1991). In the Gulf of Alaska, effects of ENSO events on seabirds have been less obvious (Piatt et al. 1999), although die-offs of thousands of adult Black-legged Kittiwakes (*Rissa tridactyla*) and Short-tailed Shearwaters (*Puffinus tenuirostris*) in the summer of 1983 (Hatch 1987) and of more than

100 000 Common Murres in 1993 (Piatt and Van Pelt 1997) may have been associated with ENSO events. The results reported here for Hecate Strait indicate that ENSO conditions may also affect seabird reproduction in northern British Columbia waters.

Ancient Murrelet breeding success was affected by March SST and the regression slope of chick mass on date was affected by May SST. The relationship between March SST and reproductive success is not surprising because breeding success is primarily determined by whether or not females desert their clutches early in incubation (the first half of April), following the effort of egg production (Gaston 1992). In 1998, an unusually large number of desertions occurred after the first egg was laid (26% of breeding pairs, 63% of all desertions). Adult Ancient Murrelets may have arrived to breed in Laskeek Bay in poor condition, if prevailing oceanographic conditions in their wintering areas had caused a reduction in suitable food supplies. While it is not uncommon for Ancient Murrelets to abandon one egg, it is rare for them to desert after both eggs are laid (Gaston 1992). In 1998, two pairs abandoned their nest after incubation started. The additional desertions after incubation had begun may indicate that food was difficult to find near the colony.

Chick mass at departure is determined principally by the number of days that the chick remains in the burrow between hatching and departure, because chicks are not fed during that period and lose approximately 6% of their body mass daily (Gaston 1992). The length of time that chicks spend in the burrow before departure is probably determined by the frequency of brooding changeovers between parents. Brooding shifts can last several days (Sealy 1975; Gaston and Powell 1989) and are presumably related to feeding conditions at sea. Chick departure normally occurs only in the presence of both parents. Hence, an increase in the length of brooding shifts will increase the mean time that the chicks must remain in the burrow before departing to sea.

The positive correlation between the slope of the regres-

sion of chick mass at departure on a particular date with May SST suggests that in years with low SST in May, there was a greater contrast between early and late breeders in the time that elapsed before they took their young to sea. This apparently paradoxical result may relate to the fact that in years of high SSTs reproductive success was low, so that young or otherwise less competent birds did not complete incubation. In better years, more of these less competent birds reared chicks, accounting for the increased proportion of light chicks late in the season. This hypothesis accounts for the lack of correlation between SST and mean chick mass, as an increase in the mass of early-hatched chicks is counterbalanced by a greater number of late-hatched, light chicks.

The lack of a relationship between SST or SO index and adult mass, combined with strong effects on reproductive success, suggests that breeding birds were close to their threshold tolerance in the early stages of reproduction; apparently, birds deserted rather than continue breeding in poor condition, as suggested by Gaston and Jones (1989). The absence of any effect on egg size is surprising, but may indicate that egg size is so critical to successful reproduction in this precocial species that no trade-off with feeding conditions can occur without severe effects on fitness: if an egg is laid at all, it must be of normal size.

The advance in timing of breeding of Ancient Murrelets between 1984 and 1999 is similar to observations made on seabirds elsewhere in British Columbia (Bertram 1999). Neither the advance in timing of breeding nor the progressive reduction in chick mass at departure seen in our study can be linked directly to the oceanographic factors considered here, which have shown no secular change in northern British Columbia waters since 1983. However, for the Gulf of Alaska as a whole, SST has increased and salinity has declined over the past four decades, resulting in a shallower surface layer of mixed water and a reduction in nutrients and primary productivity (Freeland and Whitney 2000). These changes have been linked to changes in the Aleutian Low Pressure Index (Beamish et al. 1995), the North Pacific Index (Trenberth and Hurrell 1995), and other large-scale ocean/climate indices, all of which have shown similar trends over the past 50 years (Beamish et al. 1999b). These longer term changes have been correlated with changes in fish populations (Beamish and Bouillon 1993; Sugimoto and Tadokoro 1997; Beamish et al. 1999a). However, the period considered here is too short to test whether observed changes in Ancient Murrelet breeding biology can be linked to these longer term oceanographic cycles.

Changes in primary productivity over recent decades have led to earlier and smaller peaks in zooplankton stocks (Mackas et al. 1998). The advance in the date of peak zooplankton availability has been identified by Bertram et al. (2000) as a possible cause of declines in population indices for Cassin's Auklets breeding at Triangle Island in Queen Charlotte Sound. They suggested that the auklets have not been able to breed early enough to take advantage of the peak abundance of prey; hence, a mismatch in timing of breeding has developed.

Without information on timing and abundance of prey stocks available to them, we cannot evaluate this possibility for Ancient Murrelets. However, the advance in laying date and reduction in chick mass at departure observed for An-

cient Murrelets could relate to a deterioration in conditions for feeding because of lower availability of zooplankton prey. For Ancient Murrelets, further reductions in chick mass at departure may eventually lead to reduced recruitment, as the survival of chicks from the lower end of the departure-mass distribution is poor (Gaston 1997). Both these lines of evidence suggest that environmental conditions over recent decades have deteriorated for populations of planktivorous auks breeding on the coast of British Columbia. As these populations constitute major fractions of the species' global populations (Rodway 1991), this finding is of considerable conservation concern.

Acknowledgments

Many people helped to gather Ancient Murrelet data, most of them volunteers. We especially thank the following for their contribution: on East Limestone Island, Andrea Lawrence, Janet Brown, Virginia Collins, Colin French, Janet Grey, Kathy Heise, and Laskeek Bay Conservation Society Directors Kevin Borserio, Charlotte Husband, Keith Moore, and Maggie Stronge; on Reef Island, Christine Adkins, David Duncan, Joelle Fournier, Kathy Heise, Ian Jones, Andrea Lawrence, David Noble, David Powell, Stephen Smith, and Yves Turcotte. Additional people that we thank are Al Eadie, Lorne MacIntosh, and Greg Martin. Alan Burger kindly supplied information on other seabirds in British Columbia and provided comments on the manuscript, which also benefited from extensive suggestions by an anonymous reviewer. This study was generously supported by the Canadian Wildlife Service, W. Alton Jones Foundation, South Moresby Forest Renewal Account, and Gwaii Trust, with permits from the British Columbia Ministry of Environment, Lands and Parks and the Archipelago Management Board. We are most grateful to the Institute of Ocean Sciences, Sidney, B.C., for making their oceanographic data available so conveniently and at no cost.

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