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# Effects of interdecadal climate variability on marine trophic interactions: rhinoceros auklets and their fish prey

April Hedd[1, 3, *], Douglas F. Bertram[1, 2, 4], John L. Ryder[1, 5], Ian L. Jones[1, 6]

[1]Simon Fraser University, Centre for Wildlife Ecology, Department of Biological Sciences, 8888 University Drive, Burnaby, British Columbia V5A 1S6, Canada

[2]Environment Canada, Canadian Wildlife Service, 5421 Robertson Rd. Delta, British Columbia V4K 3N2, Canada

[3]*Present address:* Cognitive and Behavioural Ecology, Departments of Psychology and Biology, Memorial University of Newfoundland, St. John's, Newfoundland A1B 3X9, Canada

[4]*Present address:* Environment Canada, Canadian Wildlife Service, c/o Institute of Ocean Sciences, 9860 West Saanich Road, PO Box 6000, Sidney, British Columbia V8L 4B2, Canada

[5]*Present address:* Environment Canada, Canadian Wildlife Service, 5421 Robertson Rd. Delta, British Columbia V4K 3N2, Canada

[6]*Present address:* Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland A1B 3X9, Canada

ABSTRACT: This paper presents time-series information on the diet composition and breeding performance of rhinoceros auklet *Cerorhinca monocerata* at Triangle Island, British Columbia, Canada, during 15 breeding seasons between 1976 and 2001. Three shifts in ocean climate occurred within British Columbia during this period (1976–77, 1989–90, 1998–99), allowing us to evaluate associations between marine environmental conditions and the reproduction of this piscivorous seabird. Lipid-rich Pacific sand lance *Ammodytes hexapterus* was the single most important prey delivered to chicks across years (15 yr avg. 38%; annual range 4 to 86%). Interannual variability was high, but in general breeding performance was strongest when 0+ sand lance predominated chick diets. Other annually important prey taxa included Pacific saury *Cololabis saira*, juvenile rockfishes *Sebastes* spp., Pacific herring *Clupea pallasi* and juvenile salmonid *Oncorhynchus* spp. The dietary importance of these prey also varied seasonally. Marine environmental conditions (evaluated using sea surface temperatures, SSTs) were clearly associated with reproduction of rhinoceros auklet, as both occurrence of sand lance in the diet and the growth rates of chicks diminished as spring SSTs increased ($r = -0.680$, $p < 0.01$, and $r = -0.697$, $p < 0.01$, respectively). We hypothesized that recruitment to local sand lance populations was temperature dependent. The strong negative relationship between dietary occurrence of 0+ sand lance and spring SST ($r = -0.560$, $p < 0.05$), coupled with the lack of a similar relationship for 1+ sand lance ($p > 0.20$), was consistent with the temperature-dependent recruitment hypothesis. Our data suggest that SSTs could interact with population age structure to affect the recruitment dynamics of Pacific sand lance. We estimated the annual dietary importance of 0+ sand lance to rhinoceros auklets using spring SST and the importance of 0+ sand lance in the diet the previous year.

KEY WORDS: Ocean climate · Rhinoceros auklet · *Cerorhinca monocerata* · Forage fish · *Ammodytes hexapterus* · Sand lance · Rockfish · Pacific saury

## INTRODUCTION

Variation in seabird breeding performance and population size has become increasingly recognized as reflective of both naturally and anthropogenically driven fluctuations in abundance of prey (Phillips et al. 1996, Anker-Nilssen et al. 1997, Davoren & Montevecchi 2003). This is especially true when the prey are focal forage species that provide critical trophic links between zooplankton and higher-level predators.

*Email: ahedd@mun.ca

Relationships between prey abundance and seabird breeding performance have been well defined for systems such as the North Sea where forage fish (including lesser sandeel *Ammodytes marinus* and herring *Clupea harengus*) are commercially exploited in waters adjacent to monitored seabird populations (e.g. Monaghan et al. 1989, Phillips et al. 1996, Anker-Nilssen et al. 1997). In an extreme example, where few suitable alternative prey were available, fishery-induced impacts on Norwegian herring stocks resulted in a 64% decline of Atlantic puffin *Fratercula arctica* populations on Røst (Anker-Nilssen et al. 1997). That study and others (Anker-Nilssen et al. 1997, Litzow et al. 2002) have also documented short-term responses of breeding seabirds to fluctuations in prey availability involving changes in chick diet, growth and survival. A recent study has suggested climactic impacts on lesser sandeel populations in the North Sea, with warm temperatures during the egg and larval stages being associated with poorer than average recruitment (Arnott & Ruxton 2002). Understanding the underlying mechanisms is fundamental to developing predictions about possible impacts of ocean climate variation on prey stocks and the populations of upper-trophic-level predators that depend on them.

In the Northeast Pacific, El Nino Southern Oscillation (ENSO) events (every 2 to 7 yr) drive considerable interannual variability in ocean climate, while the Pacific Decadal Oscillation (PDO) characterizes fluctuations between warm- and cold-water regimes on decadal time scales (Ware 1995, Mantua et al. 1997, Hollowed et al. 2001). Ocean climate shifts associated with PDOs occurred within the Northeast Pacific in 1976–77 and in 1989–90 (Hare & Mantua 2000, McFarlane et al. 2000), and recent evidence suggests that another shift occurred in 1998–99 (McFarlane et al. 2000, Mackas et al. 2004). Sea surface temperatures (SSTs) off the south coast of British Columbia have generally increased since the 1970s and peaked in the mid to late1990s, reaching some of the highest temperatures recorded in the 20th century. SSTs dropped abruptly and significantly in 1999, coincident with the latest shift in ocean climate.

In the California current ecosystem an 80% decline in zooplankton biomass was recorded between 1951 and 1993 (Roemmich & McGowan 1995), coincident with both population declines for breeding planktivorous seabirds (Ainley et al. 1994, Bertram et al. 2000) and declines in birds at sea (Veit et al. 1996). Off the coast of British Columbia, nutrient levels in surface waters dropped precipitously during the warm period in the 1990s (Whitney et al. 1998). In both nearshore and offshore environments of British Columbia, the timing of peak zooplankton biomass advanced by 6 to 8 wk between 1975 and 1998 (Mackas et al. 1998) and was associated with reproductive failure for the planktivorous Cassin's auklet *Ptychoramphus aleuticus* due to a mismatch in the timing of reproduction and prey availability (Bertram et al. 2001). Productivity and marine survival of salmonids in British Columbia, Washington, Oregon and California were greatly reduced from the mid to late 1990s (Beamish et al. 2000, Cole 2000, Welch et al. 2000, Botsford & Lawrence 2002, Mueter et al. 2002). Coincident with the strong La Nina event in 1999, zooplankton biomass increased and the community composition changed within coastal regions of British Columbia (Mackas et al. 2001, Mackas & Galbraith 2002, Zamon & Welch 2005). In 1999, the reproductive performance of both planktivorous (Cassin's auklet) and piscivorous seabirds (rhinoceros auklet *Cerorhinca monocerata* and tufted puffin *Fratercula cirrhata*) on Triangle Island, the largest seabird colony in western Canada, improved dramatically compared to previous years in the 1990s (Bertram et al. 2001; Hedd et al. 2002; Gjerdrum et al. 2003). The trend toward improved breeding performance for these species continued through 2001.

The diet and breeding performance of the rhinoceros auklet at Triangle Island, British Columbia, was quantified in the 1970s (Vermeer & Cullen 1979, Vermeer 1980, Vermeer & Westrheim 1984), the 1980s (Bertram & Kaiser 1993) and the 1990s (Bertram et al. 2001), but the time-series have never been collated and analysed together. In this paper, we examine data from 15 breeding seasons spanning 1976–2001 to explore relationships between chick diet, breeding performance and ocean climate variation using SST as a proxy. Based upon Bertram et al. (2001) and Gjerdrum et al. (2003) we anticipated strong SST breeding performance associations and explored a number of hypotheses to explain associations between SST and availability of Pacific sand lance *Ammodytes hexapterus*, the predominant prey of breeding rhinoceros auklets at Triangle Island. Understanding the underlying mechanisms would allow us to predict the likely consequences of future ocean climate variation for rhinoceros auklet and other populations of upper-trophic-level predators which also depend on sand lance.

## MATERIALS AND METHODS

**Species and study site.** In 15 breeding seasons between 1976 and 2001, we examined chick diet and breeding performance of the rhinoceros auklet at Triangle Island (Fig. 1; 50° 52′ N, 129° 05′ W; hereafter Triangle). Rhinoceros auklets are medium-sized (520 g) alcids that provision chicks mainly with fish over 45 to 65 d, after which time chicks fledge at 30 to 80% of adult body mass (Vermeer & Cullen 1979, this study).

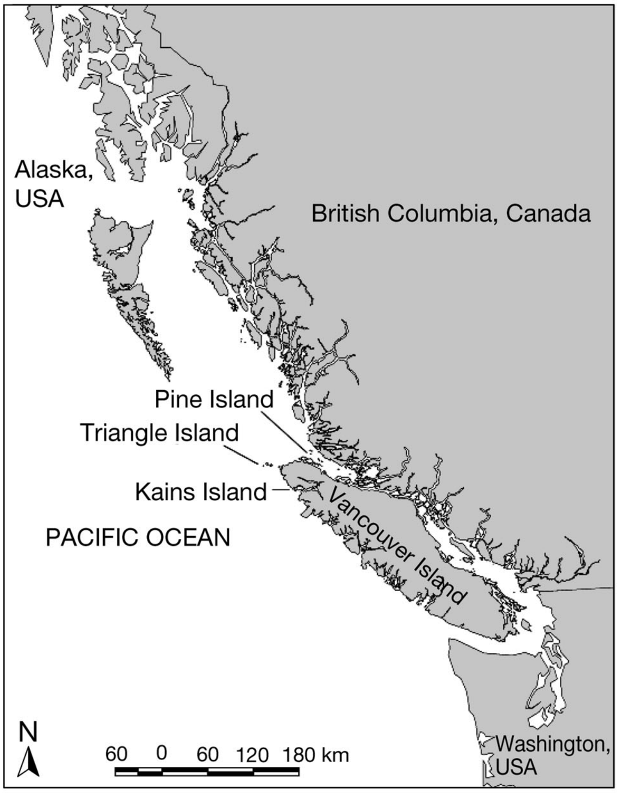

Fig 1. Map of British Columbia coast, showing location of Triangle, Pine, and Kains Islands

Adult birds can dive to 60 m (Burger et al. 1993, Kato et al. 2003, Kuroki et al. 2003), but those from local populations spend much of their time at sea within the upper 10 m of the water column (Burger et al. 1993). The foraging range of breeding rhinoceros auklets at Triangle is ca. 60 km (McFarlane Tranquilla et al. 2005). Adults arrive at the colony at night to provision chicks carrying multiple prey items crosswise in their bills (termed 'bill loads'). In 1989, the rhinoceros auklet population on Triangle was the second largest within Canada, estimated at 41,682 breeding pairs (Rodway 1991).

**Physical oceanography: SST at Pine Island.** Mean monthly SSTs at Pine Island (50° 58′ N, 127° 41′ W; Fig. 1), 94 km east of Triangle, were used to characterize physical oceanographic conditions within the area (Institute of Ocean Sciences Lighthouse Data Web site: http://www-sci.pac.dfo-mpo.gc.ca/osap/ data/SearchTools/Searchlighthouse_e.htm; accessed 29 August 2005). Across the time-series of oceanographic information available (1937–2001), SSTs at Pine Island (April) strongly positively correlated with April values of the Pacific Decadal Oscillation (http://jisao.washington.edu/pdo/PDO. latest, accessed 29 August, 2005; $r = +0.784$, $n = 66$, $p < 0.001$), indicating that local SSTs are reflective of general SST variations within the Northeast Pacific ocean. Near Pine Island deep tidal mixing provides surface temperatures representative of those found throughout the water column. We extracted and averaged Pine Island SSTs across periods relevant either to the bird breeding season (April, when breeding is initiated, or May–August, which represents the entire breeding period) or to Pacific sand lance, the most important prey species at Triangle (January–March, which represents the larval/early juvenile stage, Field 1988).

**Collection of nestling food samples.** Prey items intended for chicks were collected from adults in July and August 1976–79 (sampling methods detailed in Vermeer & Westrheim 1982), in July of 1984–86 (detailed in Bertram & Kaiser 1993) and at 7 to 10 d intervals between June and August of 1994–2001. From 1994 to 2001, returning adults were spotlighted with a headlamp as they landed near their burrows and captured by hand or with a dipnet. Ten to 15 bill loads were collected per sampling night and placed in plastic bags for subsequent identification and measurement (i.e. weight and standard [SL] and/or fork length [FL]). Unidentified species were frozen or preserved in 10 to 15% formalin/seawater for later identification by Moira Galbraith (Institute of Ocean Sciences, Victoria, British Columbia). Bill loads were collected in areas where no other research was being conducted. Data from 1985 included 'burrow loads' (total food delivered to a burrow in an evening), and while these were used to describe species composition they were excluded from estimates of bill load size and numbers of prey per sample.

Sand lance were divided into 2 age classes following Vermeer & Westrheim (1984); fish from 40 to 110 mm FL were assumed to be 0+ (1st year) fish, while those from 111 to 180 mm were assumed to be 1+ (2nd year) fish. We used forward stepwise regression to determine if the dietary occurrence of age 0+ sand lance in year $x$ could be estimated from SST and the presumed age structure of the sand lance population in year $x$–1 (see Arnott & Ruxton 2002). In our analyses we used the dietary importance of 0+ sand lance in year $x$–1 as a proxy for the relative abundance of 1+ fish the following year. Age-class assignment of Pacific herring was based upon SL, using data from Quatsino Sound, west coast of Vancouver Island (J. F. Schweigert pers. comm.). Age-class assignments for other fish species were based upon literature accounts (see references in Table 1). Diets were examined largely as % mass, but also % number for some analyses involving prey age structure. Unless otherwise stated, percentages describe all samples collected between June and August.

**Breeding performance**. Rhinoceros auklet breeding performance was assessed from chick growth rate and fledging mass (age at fledging was also estimated). Hatching success and breeding propensity were not assessed because these measures were not available for some years and because the sampling methodology changed over time. Sampling methods for estimating chick growth from 1976–78 were described by Vermeer et al. (1979), while Bertram et al. (1991) described the methods from 1984–86. Between 1994 and 2001 occupied burrows were checked at 3 to 5 d intervals prelaying, after 30 to 35 d when an egg was discovered, and then at 3 to 5 d intervals until hatching. The mass (±1 g) and flattened wingchord (±1 mm) of chicks was measured at 10 d time-specific intervals in 1994 and 1995 and at age-specific intervals from 1996 to 2001 until chicks died, disappeared or fledged from the burrow. When hatch dates were unknown, nestling ages were estimated from wingchord measurements using calibration of wing length against age for a sample of known-aged chicks in 1997 (Triangle Island Research Station, unpubl. data). Wing growth can vary under different food supply conditions, but this technique allowed us to make comparisons of similar-aged chicks among years even when hatch dates were unknown. It is most reliable when conducted early in development, and in all years chicks were included only if estimated to be ≤25 d old when first measured. In 1996, chicks were measured at hatch, 10, 20, 30, 40 and 45 d old and then every 2 d to fledging. From 1997 to 2001 chicks were measured at hatch and then at 10, 40 and 45 d old and every 2 d to fledging. Chicks were considered fledged if they were >40 d old when last found in the burrow.

Annual population level estimates of chick growth (g $d^{-1}$) were constructed for the linear phase of the growth cycle, defined by Bertram et al. (1991) as the period from 10 to 40 d of age. To increase the sample size for some years, this phase was extended here to 9 to 41 d. Approximate linear growth trajectories for the 1970s were calculated from daily age-specific mass data collected by K. Vermeer and colleagues. Raw data were available for 1976, while estimates for 1977 and 1978 were derived from the literature. The 1977 value represents the difference in mean chick mass at ca. 30 and 49 d old, as chicks were only measured a few weeks prior to fledging (Vermeer & Cullen 1979, Vermeer 1980). This was likely an underestimate as growth rates tend to decline as peak mass is approached (Vermeer & Cullen 1979, their Figs. 2 & 3). The difference in average fledging period and the average number of days between peak mass and fledging in 1976 and 1978 (Vermeer & Cullen 1979, their Tables 2 & 3) was used to assign 49 d as an average age at peak mass. This value was used in 1977 when no data on fledging period were available. The growth rate for 1978 represents the difference in mean chick mass at 9 and 41 d of age, derived from mean evening weights in Appendix 3 of Vermeer (1987). Data for fledging mass, age and success in the 1970s are from Vermeer & Cullen (1979).

In the 1980s and from 1994 to 2001, growth trajectories were derived from regression of mass on age for individual chicks, and the average value for the pooled data provided a single estimate each year. Information on fledging mass, age and success were not collected during the 1980s. From 1996 to 2001 fledging mass and age were calculated from the sample of chicks ≥40 d old when last present in the burrow. Because of different sampling protocols in 1994 and 1995, fledging mass and age are not directly comparable to subsequent years and are therefore not presented. Relationships between nestling diet and performance and the associations of both with SST were examined with correlational analyses. Data are presented as means ±1 SE and statistical significance was accepted at $p < 0.05$.

## RESULTS

### SST and breeding phenology of rhinoceros auklets

Spring (April) SST at Pine Island averaged 7.9 ± 0.1°C (range 6.6 to 9.5°C, Fig. 2A) between 1937 and 2001. At the outset of rhinoceros auklet studies at Tri-

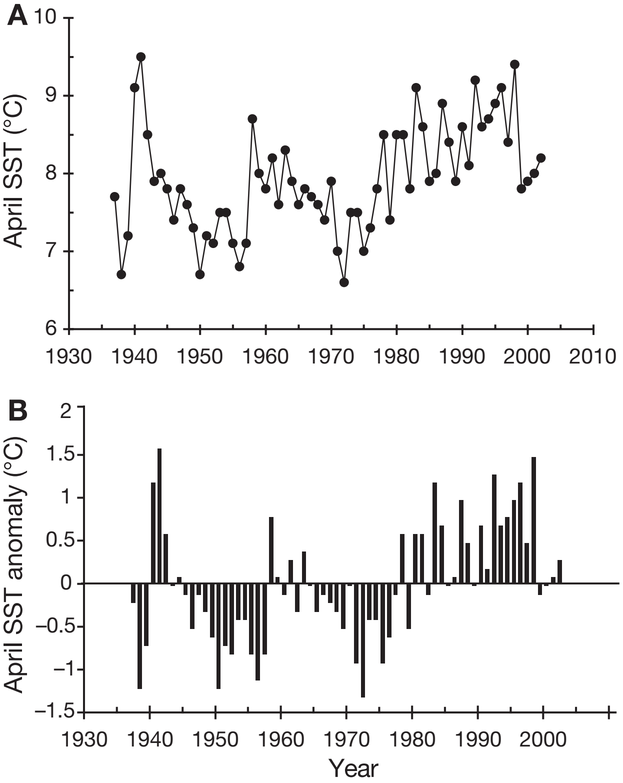

Fig. 2. (A) Mean spring (April) SST at Pine Island, British Columbia, 1937–2002 and (B) SST anomalies over same period

angle (mid-1970s), spring SSTs were relatively cool, with 1972 being the coldest year on record. Temperatures were variable, but normal to warm in the 1980s, and they warmed substantially through the 1990s (Fig. 2B). At 9.4°C, 1998 was the second warmest spring in the preceding 65 yr. An abrupt shift occurred in 1999 when the spring SST dropped below 8°C. Temperatures during 2000–01 were close to the long-term average.

Concurrent with the general shift from relatively cool to warmer waters between the 1970s and 1990s, rhinoceros auklets bred significantly earlier in the season (see also Bertram et al. 2001). Mean hatch dates in the 1970s and 1980s averaged 28 June ± 3.4 d but 14 d earlier (14 June ± 0.9 d) between 1994 and 2001 ($F_{1,12}$ = 21.93, p = 0.001). Hatch dates during this period were negatively related to spring SST ($F_{1,12}$ = 6.59, r = –0.595, p = 0.025), but, as recently demonstrated for tufted puffins at Triangle (Gjerdrum et al. 2003), hatch dates more strongly correlated with time-lagged SSTs (2 yr lag: $F_{1,12}$ = 13.58, p = 0.003, r = –0.729; 3 yr lag: $F_{1,12}$ = 7.38, p = 0.019, r = –0.617; 4 yr lag: $F_{1,12}$ = 27.20, p < 0.000, r = –0.833).

### Diet of rhinoceros auklets

1204 food samples (total mass = 29 408 g) were collected between 1976 and 2001 (Appendix 1). Bill loads averaged 26.4 ± 0.4 g (range = 0.7 to 85 g, n = 1189) and contained 6.4 ± 0.2 prey items (range = 1 to 36, n = 1191). While bill loads collected in July were largely similar in size across years, those from 1979 were significantly smaller than those from 1977, 1986, 1997 and 2001 ($F_{13,616}$ = 3.34, p < 0.001, Tukey's HSD p < 0.05). Examining only the period 1994–2001 when samples were collected from June through August, bill load mass varied within years ($F_{2,745}$ = 15.30, p < 0.001), with smaller loads delivered to chicks in June than in July or August (Tukey's HSD p < 0.001).

Fish accounted for 99 % (7849 of 7906) of all prey items and contributed more than 97 % by mass to the chick diet each year. Cephalopods constituted the remainder, occurring in 3.5 % (n = 42) of samples. Seventeen fish taxa from 15 families were identified (Appendix 1). Five dominant taxa, in decreasing order of importance, were Pacific sand lance (mean annual mass contribution = 38 %, range 4 to 86 %), Pacific saury *Cololabis saira* (24 %, range 0 to 91 %), juvenile rockfishes *Sebastes* spp. (16 %, range 0 to 57 %), Pacific herring *Clupea pallasi* (7 %, range 0 to 45 %) and juvenile salmon *Oncorhynchus* spp. (6 %, range 0 to 19 %; see Table 1 for prey size information). Together these taxa accounted for ≥88 % by mass in 13 of the 15 yr, but their relative importance varied substantially among years (Fig. 3). Sand lance (0+ and 1+ fish) was the single most important prey overall, and it predominated in the diet in 7 yr. First-year Pacific saury predominated in 1976 and contributed >40 % by mass in both 1977 and 2001. Largely 1st-year rockfish comprised

Table 1. *Cerorhinca monocerata*. Information on size and age class (0+ = 1st yr, 1+ = 2nd yr, 2+ = 3rd yr) of main prey species in diet of rhinoceros auklet chicks at Triangle Island, along with details of mean number of fish per bill load, mean bill load mass and approximate energy density of bill loads that contained a single species. In this study, 64 % of bill loads (757 of 1189) contained just 1 species. The energy content of bill loads was estimated on a wet mass basis (where wet mass energy densities were calculated from water percentage as follows: dry energy density × (1 – proportion of water); Van Pelt et al. 1997). Caloric values of prey are from Vermeer & Devito (1986), and % water content of prey is from Anthony et al. (2001). Whenever possible, energy content was derived using overall species biomass in diet broken down by age class. Sample sizes are given in parentheses

| Prey taxa | Fork length (mm) and age class | No. fish | Bill loads mass (g) | Energy content (kJ) | Source (Ageing) |
|---|---|---|---|---|---|
| Sand lance | 88 ± 0.4 (3888)<br>0+, 1+ | 8.6 ± 0.4 (289) | 24.3 ± 0.7 (289) | 130 | Vermeer & Westrheim (1984) |
| Pacific saury | 167 ± 1.7 (298)<br>0+ | 2.0 ± 0.1 (174) | 34.8 ± 0.9 (174) | 145 | Suyama et al. (1996) |
| Rockfish spp. | 60 ± 0.2 (1871)<br>0+ | 7.1 ± 0.3 (139) | 17.6 ± 0.7 (139) | 79 | Phillips (1964), Westrheim & Harling (1975) |
| Pacific herring | 129 ± 3.1 (105)<br>0+, 1+, 2+ | 1.4 ± 0.1 (51) | 34.1 ± 1.9 (51) | 202 | J. F. Schweigert (pers. comm.) |
| Sockeye salmon | 120 ± 2.3 (37)<br>1+ | – | – | | Burgner (1991) |
| Salmon spp. | 121 ± 2.0 (53) | 1.5 ± 0.1 (33) | 27.5 ± 1.7 (33) | 152 | |
| Blue-throat argentine | 99 ± 0.4 (326) | 5.4 ± 0.2 (53) | 31.8 ±1.0 (53) | 181 | |
| ANOVA for species differences | | $F_{5,734}$ = 70.16<br>p < 0.001 | $F_{5,733}$ = 44.67<br>p < 0.001 | | |

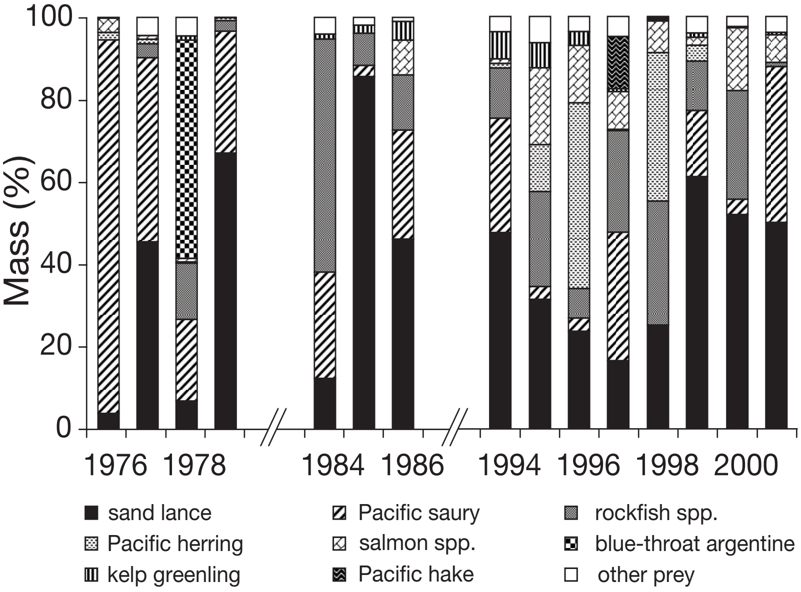

Fig. 3. Annual composition (by mass) of rhinoceros auklet nestling diet at Triangle Island, British Columbia, 1976–2001

>20% of chick diet in the 4 yr after 1994 and were the most important prey in 1984 (Fig. 3). Pacific herring contributed significantly to the diet only in the 1990s, being the most important prey both in 1996 (45% by mass; mainly 1+ fish) and 1998 (36% by mass; mainly 0+ fish). Second-year sockeye salmon *Oncorhynchus nerka* constituted ≥5% of the chick diet from 1995 to 1998, while in 1986, 1995–96, and 2000–01 unidentified juvenile salmonids accounted for an additional 7 to 15% of the diet. Unusual within the time-series was 1978, when blue-throat argentine *Nansenia candida* comprised 53% of the diet. Apart from 1998 when argentine were found in 2 samples, this species did not otherwise appear in the chick diet at Triangle. Three other species made annual mass contributions greater than 4%: kelp greenling *Hexagrammos decagrammus* (1986, 1994 and 1995), sablefish *Anoplopoma fimbria* (1977 and 1978) and Pacific hake *Merluccius productus* (1997). The 7 remaining taxa were of minor importance.

Bill load mass differed according to the type of prey delivered (Table 1). Loads composed of Pacific saury, Pacific herring and blue-throated argentine were significantly heavier than those of sand lance or rockfish (Tukey's HSD $p < 0.001$). Rockfish loads were the lightest delivered to chicks, while salmon loads were intermediate. The number of prey per bill load also differed by species (Table 1), with meals of Pacific saury, Pacific herring, and salmon consisting of a few large fish, while loads of sand lance and blue-throat argentine instead contained more, smaller fish (Tukey's HSD all $p < 0.01$).

### Breeding performance of rhinoceros auklets

Annual growth rate anomalies (Fig. 4) indicate that while chick growth was variable between 1976 and 2001, rhinoceros auklets at Triangle experienced a succession of poor years in the 1990s. Overall, growth rates averaged 5.5 ± 0.4 g d$^{-1}$, with a low of 2.6 g d$^{-1}$ in 1976 and a high of 9.1 g d$^{-1}$ in 1985 (Table 2). Mass and age at fledging and fledging success were also highly variable among years. Mean annual fledging mass was 295 ± 17 g (range 224 to 361 g), and chicks fledged at an average age of 52 ± 1 d (range 49 to 56 d). Means of fledging mass and age were not correlated across years, but they were determined together in only 8 yr. Fledging success ranged from 34 to 97% (overall average 75 ± 6%; Table 2), and there was no statistically significant relationship between success and either fledging mass or age (success vs. mass, $r = 0.548$, $n = 9$, $p = 0.124$; success vs. age, $r = -0.558$, $n = 8$, $p = 0.152$), but sample sizes were small. Annual mean chick growth rate was strongly positively related to both fledging mass ($r^2 = 0.712$, $n = 9$, $p = 0.004$) and fledging success ($r^2 = 0.667$, $n = 11$, $p = 0.002$) but unrelated to fledging age ($r^2 = 0.290$, $n = 8$, $p = 0.169$).

Strong reproductive performance of rhinoceros auklet at Triangle was dependent upon chicks receiving a diet dominated by sand lance. The annual mean growth rate of chicks and mean chick fledging success were both strongly positively related to the proportion of sand lance in the diet (Fig. 5). In this regard, 1978 was anomalous as growth was rapid when chick meals consisted largely of blue-throat argentine (Table 2). Excluding 1978, mean fledging mass was also related

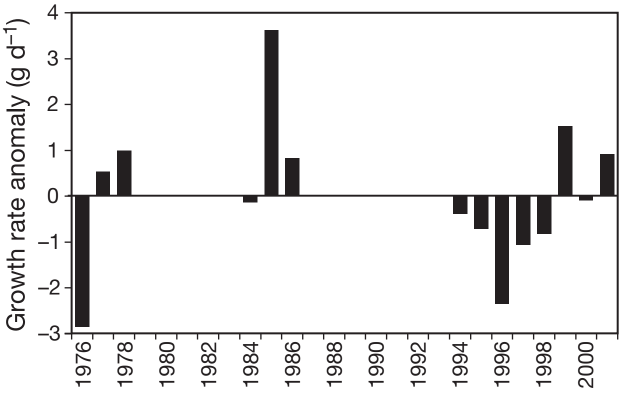

Fig. 4. Annual growth rate anomalies (g d$^{-1}$) of nestling rhinoceros auklets at Triangle Island, British Columbia, 1976–2001

Table 2. *Cerorhinca monocerata*. Summary of breeding performance of rhinoceros auklet at Triangle Island, British Columbia, 1976–2001. Growth rates (GR) were estimated between 9 and 41 d of age (see 'Materials and methods'). Sample sizes are given in parentheses, and errors are standard with the exception of fledging mass and age data from the 1970s (Vermeer & Cullen 1979) where the authors refer to 95% confidence intervals

| Year | Type of growth study | Growth rate (g $d^{-1}$) | Fledging mass (g) | Fledging age (d) | Fledging success (%) | Source and type of data analysed |
|---|---|---|---|---|---|---|
| 1976 | Daily weighing | 2.6 ± 0.4 (25) | 266 ± 20 (15) | 56 ± 4 (9) | 34 (44) | GR calculated using raw data of Vermeer & Cullen (1979); remainder from Vermeer & Cullen (1979) |
| 1977 | Daily weighing | 6.0 | 333 ± 16 (36) | – | 65 (62) | GR derived from Vermeer & Cullen (1979) and Vermeer (1980); remainder from Vermeer & Cullen (1979) |
| 1978 | Daily weighing | 6.5 | 361 ± 15 (27) | 51 ± 1 (27) | 83 (35) | GR derived from Appendix 3 Vermeer (1987); remainder from Vermeer & Cullen (1979) |
| 1984 | 10 d interval | 5.3 ± 0.2 (47) | – | – | – | GR calculated using raw data of Bertram et al. (1991) |
| 1985 | 10 d interval | 9.1 ± 0.4 (23) | – | – | – | GR calculated using raw data of Bertram et al. (1991) |
| 1986 | 10 d interval | 6.3 ± 0.4 (37) | – | – | – | GR calculated using raw data of Bertram et al. (1991) |
| 1994 | 10 d interval | 5.1 ± 0.3 (33) | – | – | 69 (36) | This study |
| 1995 | 10 d interval | 4.7 ± 0.2 (61) | – | – | 81 (73) | This study |
| 1996 | Sequential growth | 3.1 ± 0.4 (13) | 229 ± 10 (10) | 50 ± 1 (10) | 53 (15) | This study |
| 1997 | Sequential growth | 4.4 ± 0.1 (37) | 224 ± 8 (44) | 52 ± 1 (44) | 70 (57) | This study |
| 1998 | Sequential growth | 4.6 ± 0.2 (28) | 255 ± 10 (27) | 52 ± 1 (27) | 82 (34) | This study |
| 1999 | Sequential growth | 7.0 ± 0.3 (36) | 341 ± 7 (35) | 49 ± 1 (35) | 97 (36) | This study |
| 2000 | Sequential growth | 5.4 ± 0.2 (40) | 310 ± 7 (38) | 52 ± 1 (39) | 95 (39) | This study |
| 2001 | Sequential growth | 6.4 ± 0.2 (40) | 334 ± 5 (41) | 52 ± 1 (41) | 96 (44) | This study |
| | Mean ± SE | 5.5 ± 0.4 | 295 ± 17 | 52 ± 1 | 75 ± 6 | |

to the proportion of sand lance in chick diet (Fig. 5C; without 1978, $r = 0.845$, $p < 0.01$). Reproductive performance was largely independent of the other main prey types, with the exception of a negative relationship between Pacific saury and fledging success ($r = –0.616$, $p = 0.044$, $y = –0.450x + 86.420$).

### Associations between spring SST, diet composition and breeding performance

There were strong associations between spring SST and both the diet composition and breeding performance of rhinoceros auklets at Triangle. We found a significant decline in the annual proportion of sand lance in the diet and a consequent decline in chick growth rate as spring SSTs increased (Fig. 6). When spring SST at Pine Island was ≤8°C, sand lance accounted for ≥45% of the diet and chicks grew rapidly. Excluded from this regression was the extreme outlier of 1976, when April SST was 7.3°C, yet sand lance accounted for just 3.7% of the diet. Fledging mass also tended to decline with increasing SST, but this relationship was not significant ($r^2 = 0.431$, $p = 0.077$). Fledging success and spring SSTs were unrelated ($r^2 = 0.192$, $p = 0.205$).

Regardless of the dietary measure used, the contribution of age 0+ sand lance to rhinoceros auklet chick diet declined as spring SST increased (annual % mass and % number, respectively: $r = –0.560$, $p = 0.037$; $r = –0.617$, $p = 0.019$; July% mass and % number, respectively: $r = –0.621$, $p = 0.018$; $r = –0.599$, $p = 0.024$). In contrast, the contribution of age 1+ sand lance to the diet was independent of spring SST (all $p > 0.21$). Also, consistent with density-dependent relationships reported for lesser sandeel (Arnott & Ruxton 2002), we found significant negative lag–1 autocorrelations between the % number of 0+ sand lance in the rhinoceros auklet chick diet in adjacent years (annual autocorrelation: $n = –0.558$, $p = 0.003$; July autocorrelation: $n = –0.390$, $p = 0.038$). This means that the % number of 0+ sand lance in the diet was negatively related to the % number present the year before. There were similar negative autocorrelations for diet data when expressed as % mass, but these were significant only for annual measures (autocorrelation: $n = –0.399$, $p = 0.034$).

There were further associations between spring SSTs and the fish prey that augmented chick diet in the absence of sand lance. Pacific saury also occurred in years when spring SSTs were cool, peaking at 91% by mass in 1976, the year with both the coldest spring and overall breeding season SSTs. While spring SST

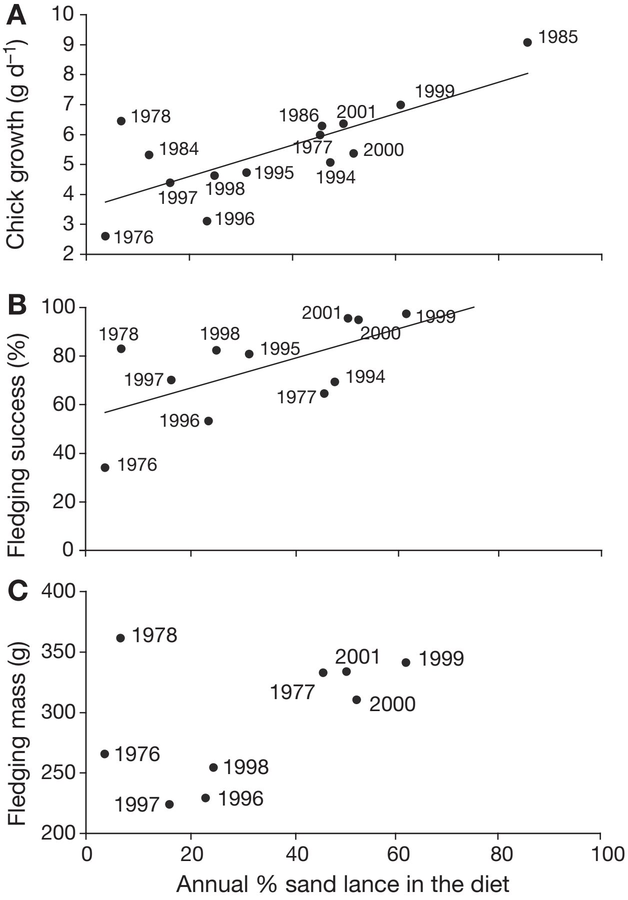

Fig. 5. Relationships between annual proportion of sand lance in nestling diet and (A) mean growth rate of chicks ($r^2 = 0.560$, $p < 0.01$, $y = 0.0524x + 3.5578$), (B) chick fledging success ($r^2 = 0.386$, $p < 0.05$, $y = 0.\ 6215x + 54.584$) and (C) chick fledging mass at Triangle Island, British Columbia

accounted for only 36% of the annual variation of Pacific saury in chick diet (Fig. 7A), this species was all but absent when spring SSTs at Pine Island exceeded 8.9°C (annually <3% by mass). The dietary contribution of rockfish and herring, in contrast, tended to increase with increasing spring SST (Fig. 7B,C). Rockfish was dominant in 1984 when the spring SST was 8.6°C. Herring formed an important part of the diet only in the 2 warmest years (1996 and 1998) when spring SSTs at Pine Island exceeded 9°C.

### Associations between SST and within-season diet variation

Along with the substantial dietary variation among years highlighted in this paper, the diet of rhinoceros auklets at Triangle also showed considerable variation within years. Broadly, these trends involved sand lance early in the season (at varying levels of dominance) with a switch to other prey as the breeding season progressed. In 10 of our 15 study years there were sufficient diet sampling dates to examine whether within-season variation in sand lance was associated with daily variation in SST. We used temperature data from both Pine and Kains (50° 16′ N, 128° 1′ W) Islands to evaluate associations, as data from Kains Island are more representative of variation at the surface. We found limited association, with significant negative correlations for 3 yr using data from Kains Island, and for just 1 yr using data from Pine Island. Pooling across 10 yr produced significant negative correlations between daily % sand lance and daily SST (Kains Island: $r = -0.533$, $p < 0.001$; Pine Island: $r = -0.507$, $p < 0.01$) but with high variability. For temperatures between 14 and 14.5°C at Kains Island, for example, the % sand lance in the diet ranged from 0 to 74%. Variation was similarly high at Pine Island. Overall, SST accounted for 26 to 28% of the daily variation in % sand lance in the diet.

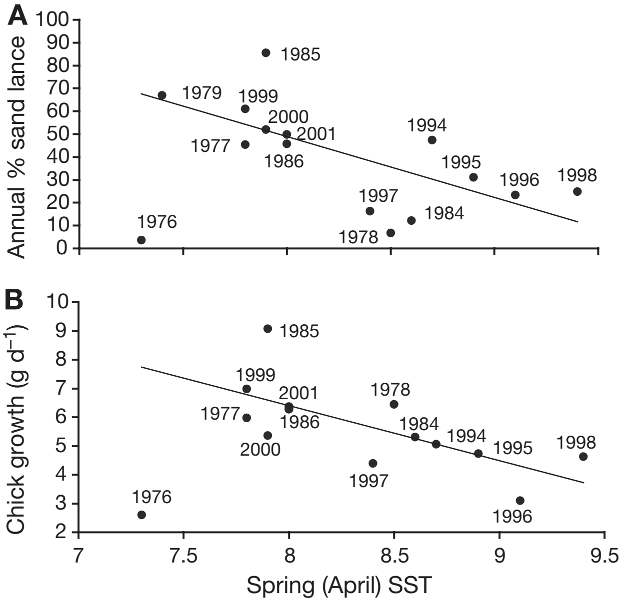

Fig. 6. Relationships between spring (April) SST at Pine Island and (A) estimated annual proportion of sand lance in nestling diet ($r^2 = 0.462$, $p < 0.01$, $y = -26.627x + 262.009$) and (B) annual growth rate of chicks ($r^2 = 0.486$, $p < 0.01$, $y = -1.9091x + 21.676$) at Triangle Island, British Columbia

### Estimating annual dietary occurrence of 0+ sand lance

We used forward stepwise regression to estimate the occurrence of 0+ sand lance (SL) in rhinoceros auklet chick diet in year *x* (by % number and % mass) using various measures of SST [(1) Spring (April), (2) breeding season (May–August) and (3) larval/early juvenile stage for sand lance (January–March)], along with the

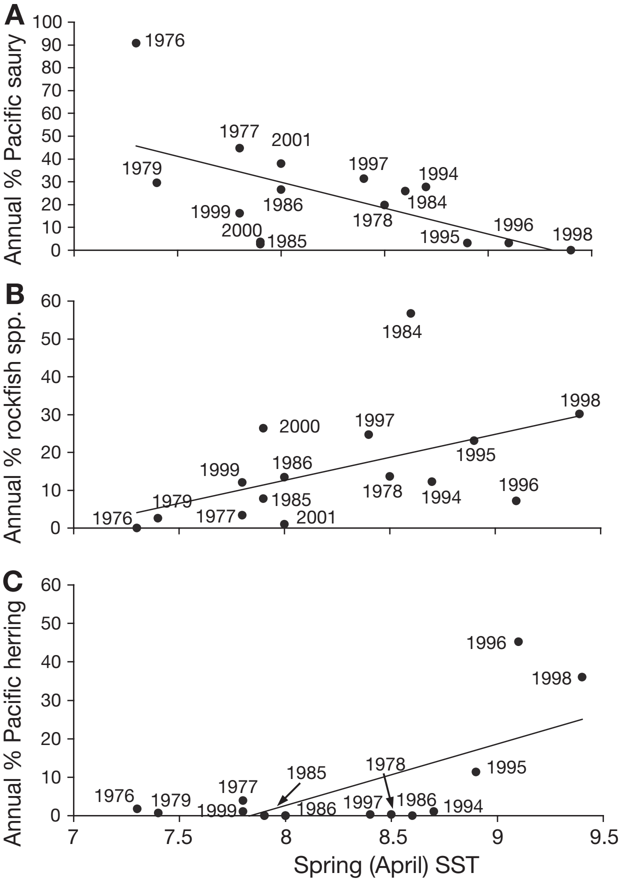

Fig. 7. Relationships between spring (April) SST at Pine Island and estimated annual proportions of (A) Pacific saury ($r^2 = 0.360$, $p = 0.018$, $y = -22.712x + 211.500$), (B) rockfish spp. ($r^2 = 0.253$, $p = 0.056$, $y = 12.177x - 84.804$) and (C) Pacific herring ($r^2 = 0.473$, $p < 0.01$, $y = 15.847x - 123.897$) in diet of nestling rhinoceros auklets at Triangle Island, British Columbia

dietary importance of the 0+ cohort in the previous year ($x$–1). All percent data were arcsine transformed prior to analysis. Details of the equations follow.

Annual dietary measures:

$$\arcsin \% \text{ number } 0+ \text{ SL} = -0.229(\text{April SST}) - 0.224\,(\text{breeding season SST}) - 0.727(\arcsin \% \text{ number } 0+ \text{ SL } x-1) + 4.910 \tag{1}$$

$r^2 = 0.917$, $p < 0.001$

$$\arcsin \% \text{ mass } 0+ \text{ SL} = -0.269(\text{April SST}) - 0.463(\arcsin \% \text{ number } 0+ \text{ SL } x-1) + 2.694 \tag{2}$$

$r^2 = 0.628$, $p = 0.019$

July dietary measures:

$$\arcsin \% \text{ number } 0+ \text{ SL} = -0.631(\text{breeding season SST}) -0.600(\arcsin \% \text{ number } 0+ \text{ SL } x-1) + 6.906 \tag{3}$$

$r^2 = 0.878$, $p < 0.001$

$$\arcsin \% \text{ mass } 0+ \text{ SL} = -0.376(\text{April SST}) - 0.373(\arcsin \% \text{ number } 0+ \text{ SL } x-1) + 3.558 \tag{4}$$

$r^2 = 0.649$, $p = 0.015$

Annual variation in dietary occurrence of 0+ sand lance was significantly related to the dietary importance of 0+ sand lance in year $x$–1 (suggesting density dependence in the sand lance population) and SSTs. These relationships form the basis to evaluate mechanistic linkages and to develop predictions about breeding performance of rhinoceros auklets in relation to SST variability.

## DISCUSSION

This paper presents a retrospective analysis of time-series information on the diet composition and breeding performance of a pursuit-diving piscivorous marine bird, the rhinoceros auklet, spanning 3 decades (1976–2001) and encompassing 3 shifts in ocean climate in British Columbia. SSTs during the study period were highly variable and spanned extremes in the 65 yr temperature record. Our main findings were strong associations between SST, prey species selected for offspring provisioning and the breeding performance of rhinoceros auklets at Triangle Island, the largest and most diverse seabird breeding colony on Canada's west coast. While we do not have sufficient annual data to examine the 1976–77 or 1989–91 regime shifts, the annual time-series initiated in the 1990s allowed us to bound the 1997–98 ENSO and the shift in ocean climate in 1999. The abrupt change in 1999 and reported impacts on zooplankton community composition (Mackas et al. 2001) were reflected as dietary shifts and improved breeding performance in the Triangle seabird community (Bertram et al. 2001, Hedd et al. 2002, Gjerdrum et al. 2003).

Variations in SST were clearly associated with the diet composition of rhinoceros auklets, demonstrating that, when conditions were cool, sand lance (particularly 0+ age fish) dominated the diet and breeding performance was strongest. The mechanism for stronger performance with increased sand lance is uncertain, but in general seabird growth and breeding performance is enhanced when chicks are fed high lipid fish (Hunt et al. 1996, Golet et al. 2000, Takahashi et al. 2001, Litzow et al. 2002). While age 0+ sand lance and rockfish (which is associated with poor breeding performance at Triangle) have similar energy densities (3.18 and 2.97 kJ $g^{-1}$ wet mass, Van Pelt et al. 1997; 19.68 and 21.77 kJ $g^{-1}$ dry mass, Vermeer & Devito 1986), our observation of stronger performance with sand lance is consistent with the 40% increase in energy delivered per bill load (Table 1). The 40% energy increase resulted both from larger sized meals and the higher energy density of 1+ sand lance (4.95 kJ $g^{-1}$ wet mass, Van Pelt et al. 1997), as this age class comprised 43% of sand lance biomass at Triangle.

Despite the high energy content of all other delivered prey (i.e. Pacific saury, Pacific herring and salmon; Table 1), blue-throat argentine was the only alternate species that resulted in rapid nestling development at Triangle. At the Seabirds Rocks colony, southern British Columbia, rhinoceros auklet chicks grew well when fed Pacific herring and salmon (Bertram et al. 2002), perhaps suggesting that rates of delivery of these particular prey to Triangle are lower. Prey size and timing of availability likely also contributed to the observed patterns of nestling performance. While large fish efficiently provision older nestlings, their sheer bulk can result in mortality for younger chicks, as reported for the large Pacific saury delivered to Triangle in 1976 (Vermeer 1980). In this study, meals of Pacific saury, Pacific herring and salmon contained a few, often very large fish (Table 1), while meals of species associated with strong growth (blue-throat argentine and sand lance) contained multiple, smaller fish. Whether rates of delivery of alternate prey are lower at Triangle or their size/age classes are inappropriate, few prey other than sand lance have been associated with successful reproduction for rhinoceros auklet at this site.

The favourable association between sand lance and breeding performance at Triangle, coupled with the lack of similar positive associations for other prey, suggests that, if available, rhinoceros auklets would likely choose sand lance for their chicks. Sand lance are abundant during spring and summer in shallow inshore, shelf areas in depths to 100 m (Reay 1970, Field 1988). They alternate between lying buried in the substrate and swimming in pelagic schools and are found in association with sandy or fine-gravel substrates (Hart 1973). Below we briefly review the habitat and temperature associations for the alternate prey species of rhinoceros auklets at Triangle and briefly discuss their reproductive implications.

## Prey fish species

Although variable, Pacific saury has contributed to the chick diet of rhinoceros auklet at Triangle in many years (Fig. 3), and it has been particularly important late in the season. Juvenile Pacific saury are epipelagic and found in association with warm, offshore water masses from California to Japan (Hart 1973). Causes of the late season shift to Pacific saury are unclear but may be linked to seasonal water mass movements. Pacific saury of the size range delivered to rhinoceros auklet nestlings have been captured by surface trawl surveys in early August, west of Cape Scott off the northwest coast of Vancouver Island (Cooke et al. 1991), and well within the foraging distances of auklet parents (McFarlane Tranquilla et al. 2005). Although their within-season appearance was associated with warmer waters (as Pacific saury was generally delivered in August), we detected a negative association with spring SST. This species was virtually absent in the years when spring SSTs exceeded 8.9°C. Perhaps similar to sand lance (see below), strong year classes were favoured when primary productivity of the ocean was high and spring SSTs were cool. The significant negative association between fledging success and importance of Pacific saury in the diet suggests it was utilized in years when prey more suitable for chick provisioning were scarce.

There was a general increase between the 1970s and early 2000s in the importance of rockfish in the diet of rhinoceros auklet at Triangle. Rockfish were a minor dietary component in the 1970s; they constituted >50% of the diet in 1984 and have been an important dietary component (>20%) in 4 yr since 1994. They were inconsequential at a number of other colonies along the British Columbia coast between 1995 and 1998 (Seabird Rocks and SG̲aang Gwaii, Queen Charlotte Islands), likely reflecting geographic variation in the species composition of local fish fauna (Bertram et al. 2002). Although we have no information on where the rockfish originated, they could have been obtained quite close to the breeding colony as waters surrounding the Scott Islands are within a Rockfish Conservation Area (Area 111, Scott Islands) protected from all rockfish harvesting by Fisheries and Oceans Canada (www.pac.dfo-mpo.gc.ca./recfish/Restricted_Areas/Rockfish_Maps_2004/MgmtAreas2004/coordinate_pages/049_e.htm, accessed 26 August 2005). At Triangle, consumption of rockfish occurred in warmer years and was associated with poor chick growth. Meals comprised solely of rockfish were lighter than average, a feature attributed to the body morphology of the genus (i.e. auklets had difficulty carrying many individuals of this relatively small, deep-bodied fish, Bertram et al. 2002). Depressed nestling growth was also observed for rhinoceros auklet on Pine Island in the 1980s (Bertram et al. 1991), when rockfish comprised a significant proportion of the diet (Bertram & Kaiser 1993).

One and 2 yr old Pacific herring contributed to the chick diet at Triangle in the 1990s, particularly 1996 and 1998, 2 of the warmest and poorest reproductive years in our time-series. Similar to sand lance, juvenile herring are found over the shelf and are numerous inshore in their first year (Hourston 1958, 1959). They are important prey for many seabirds, marine mammals and fish in the region (Schweigert 1997). The increased occurrence of 2 yr old herring in rhinoceros auklet chick diet in 1996 was supported by independent stock assessment, as the 1994 year class was the strongest seen off the west coast of Vancouver Island in 2 decades (J. F. Schweigert pers. comm.). The increased importance of herring in years when sand lance are rare in chick diet could indicate that birds adjust their search to more coastal areas when ocean prey are scarce.

Juvenile salmon contributed more to the diet of rhinoceros auklet at Triangle in the 1990s and early 2000s (annual average 9.3%) than they did in the 1970s (1.8%) or 1980s (2.8%). In summer, juvenile salmon can be found close to shore, migrating in a narrow band within 30 km of the coast before moving offshore to feed in the North Pacific (Hartt & Dell 1986). Blue-throat argentine was the only alternate prey resulting in strong chick growth for rhinoceros auklets at Triangle, but it appeared in the diet only in 1978 (except for 2 meals in 1998). Blue-throat argentine is a cold-water, bathypelagic species (Hart 1973) that was apparently locally abundant in 1978. In 1978 it was a major prey of chinook *Oncorhynchus tshawytscha* and sockeye salmon along the northeast coast of Vancouver Island (Vermeer & Westrheim 1984, A. Ostrom pers. comm.), when it was also found in rhinoceros auklet nestling diets at Pine Island (Vermeer & Westrheim 1984). Like the auklets, occurrence of this species in salmon diets was unusual and had not been recorded previously.

Apart from suggesting that rhinoceros auklets would choose sand lance if available, it was unclear if exposure to different water masses resulted in the variable patterns of prey selection observed or if different oceanographic conditions resulted in variable avian search strategies. While beyond the scope of this paper, investigation of the fish species assemblages delivered to rhinoceros auklet chicks under various SST conditions may provide additional insight into ecosystem response. Clearly, strong breeding performance for the rhinoceros auklet was associated with cool SSTs. The declines in breeding performance observed with increasing SST have also been demonstrated for Cassin's auklet (Bertram et al. 2001) and tufted puffin (Gjerdrum et al. 2003) at Triangle. Bertram et al. (2001) suggested that temperature-performance relationships could be used to predict the effects of future climate change on seabird populations. Such predictions are powerful if the underlying mechanisms and processes are understood. For rhinoceros auklet, prediction involves understanding the linkages between SST and availability of their dominant prey, sand lance, near Triangle. There are no independent data on sand lance populations, but below we assess a number of hypotheses to explain how SST could influence sand lance availability to rhinoceros auklets.

### Temperature-related hypotheses explaining sand lance variation in chick diet

#### H1: Recruitment of sand lance around Triangle increases at cooler temperatures

The strong negative relationship between spring SST and the annual importance of 0+ sand lance in rhinoceros auklet chick diet and the lack of a similar relationship for 1+ sand lance supports the recruitment-temperature hypothesis. The anomalous 1976 data point (low spring SST, few sand lance) led Bertram et al. (2001) to suggest that sand lance recruitment could be dome-shaped in relation to ocean temperature, as demonstrated for rock sole *Lepidopsetta bilineata* (Fargo & McKinnell 1989) with poor recruitment at high and low spring SST and favourable recruitment at intermediate SSTs. A 16 yr time-series for tufted puffins, for which sand lance is also a focal prey species at Triangle, indicates a bell-shaped curve between fledging success and breeding season SST (Gjerdrum et al. 2003), providing further support for a dome-shaped recruitment function for sand lance.

Annual recruitment of *Ammodytes* is highly variable and associated with temperature fluctuations at other sites (Hamada 1966, Arnott & Ruxton 2002). In the North Sea, poor recruitment has been associated with above-average ocean temperatures during the egg and larval stages (Arnott & Ruxton 2002), an effect most pronounced near the southern end of the species' range. Hamada (1966) also demonstrated temperature-recruitment associations for Japanese sand lance *Ammodytes personatus*, where increased fishery catches of 0+ fish correlated with low water temperatures during spawning.

The superior reproductive performance of Triangle seabirds in cool years has been proposed to operate through effects on the timing of zooplankton availability, in particular *Neocalanus* copepods, relative to the time of seabird breeding (Bertram et al. 2001). In years when spring was early and warm, zooplankton biomass both peaked and ended early, resulting in a mismatch between predator and prey. Alternatively, in cool years the temporal availability of copepods in surface waters was extended, providing a better match with seabird requirements. Irrespective of seasonal timing, cool ocean temperatures near Triangle also reflect conditions of well-mixed nutrients and increased primary productivity of the ocean (e.g. Beamish et al. 1999). We would expect greater overall zooplankton abundance in cool-water years, favouring planktivorous seabirds directly (e.g. Jones et al. 2002). Moreover, we also see rapid nestling growth for piscivorous rhinoceros auklets (this study and Bertram et al. 2001) and tufted puffins (Gjerdrum et al. 2003) in cool years when diets are dominated by 0+ sand lance. As sand lance themselves feed primarily on copepods (Field 1988), cool years would provide favourable feeding conditions for young fish and thus contribute to strong recruitment to local populations (see also Wright & Bailey 1996). In British Columbia, Pacific sand lance are within the southern third of their range (Hart 1973), and, based upon Myers' (1998) assertion regarding environment-recruitment relationships, we expect the proposed associations between spring SST, copepod availability and sand lance recruitment to hold in this system across years.

### H2: Spatial distribution of sand lance is temperature dependent

Warming SSTs could induce horizontal or vertical shifts in sand lance distribution that could affect their availability to rhinoceros auklets. On the Newfoundland Grand Banks Northern sand lance *Ammodytes dubius* moved to deeper (cooler) waters as temperatures increased in summer (Winters 1983) and Japanese sand lance burrowed in the sand and became dormant when water temperatures exceeded 20°C (Nagoshi & Sano 1979). While similar distributional shifts could plausibly explain patterns of sand lance occurrence in rhinoceros auklet diet (see Gjerdrum et al. 2003), our data did not provide strong support for this interpretation. Within the temperature range observed, there was little indication of a boundary above which sand lance became unavailable to the auklets; however, as occurrence declined with increasing temperature, it is possible that further temperature increases could have induced distributional shifts. In this study, the initial seasonal dominance of sand lance, its temporal persistence and species replacements were highly variable among years, collectively supporting the interpretation that they relate more to between- than within-season temperature fluctuations.

### H3: Predation intensity on sand lance increases with increasing temperature

Almost every marine piscivore in British Columbia feeds on sand lance, and distributional shifts in response to temperature could increase the diversity and/or abundance of sand lance predators (e.g. Pacific hake, Benson et al. 2002), thereby limiting its availability to rhinoceros auklets. While changing species assemblages and competitive interactions for common prey could reduce sand lance availability to rhinoceros auklets, the lack of information on sand lance population size and the impact of all its predators make this hypothesis difficult to evaluate.

While these, and likely numerous other, hypotheses could account for observed patterns of sand lance in the rhinoceros auklet diet, we suspect that the most likely scenario relates to both temperature effects on sand lance recruitment and density-dependent population processes. Ocean temperatures influence both the abundance and temporal persistence of zooplankton in surface waters, which likely affects prey availability to and perhaps survival of 0+ sand lance. As demonstrated for *Ammodytes* elsewhere (Arnott & Ruxton 2002), 0+ sand lance off British Columbia appear to be affected by population age structure. Annual dietary occurrence of 0+ sand lance for rhinoceros auklets could be estimated from SSTs combined with an index of 0+ sand lance abundance the previous year. This concurs with Arnott & Ruxton (2002), who demonstrated negative relationships between lesser sandeel recruitment and both ocean temperature and population size of 1+ sandeels. For lesser sandeel the density-dependent effects imposed by 1+ fish were largely responsible for alternating years of high and low recruitment. Physical disturbance of the spawning bed by burrowing adults and juveniles was suggested as a possible mechanism, as adults do not use separate spawning grounds (Reay 1970, Arnott & Ruxton 2002). Juvenile and adult lesser sandeels may also cannibalize eggs or hatching larvae, but this explanation seems unlikely for Pacific sand lance, as Robards & Piatt (1999) suggested it is not cannibalistic.

## CONCLUSIONS

The time-series data sets assembled here for rhinoceros auklet combined with those for Cassin's auklet (Bertram et al. 2001) and tufted puffin (Gjerdrum et al. 2003) highlight how impacts of ocean climate variation on prey populations result in large interannual variation of seabird breeding performance at Triangle. Negative relationships between spring SST and chick growth were demonstrated for both rhinoceros and Cassin's auklets, and a dome-shaped relationship was found for tufted puffins, where growth was maximal at intermediate temperatures (Gjerdrum et al. 2003). For rhinoceros auklets the predictive linear SST breeding performance model (Bertram et al. 2001) likely reflects linkages between climate, ocean productivity, sand lance recruitment and their availability to breeding seabirds. Our results are consistent with both climatic and population age structure effects on sand lance and provide a basis for investigating mechanisms that underpin variation in recruitment and population size of this focal species.

Extremely poor breeding performance for all seabird species in the warmest years (1996 and 1998) suggests climate-trophic linkages for both piscivores and planktivores (Bertram et al. 2001, Hedd et al. 2002, Gjerdrum et al. 2003, this study). Only the tufted puffin, however, exhibited near complete breeding failure in the warmest years, suggesting a sensitivity that surpassed that of the other species. Puffins tend to be diurnal foragers that provision young multiple times per day, a strategy that restricts parental foraging range (Ostrand et al. 1998). In contrast, each rhinoceros auklet parent provisions its young at most once per night (max. 2 feeds $d^{-1}$) and has the capacity to search for prey at broader geographic scales. Rhinoceros auklets may also feed on diel vertically migrating species such as herring that may be less available to puffins during the day.

The striking and consistently negative effects of ocean warming on the breeding performance of seabird species within the Triangle community warrant further development on the use of seabirds as indicators of climate change. Seabird time-series data provide relatively inexpensive information about the responses of upper-trophic-level predators to ocean climate variability. The relative ease with which dietary and reproductive information can be collected from seabirds, and the trophic insights gained, necessitates incorporating seabird colony studies as an integral part of any marine ecosystem monitoring program.

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**Appendix 1.** *Cerorhinca monocerata*. Diet (annual mass, %) of rhinoceros auklet at Triangle Island, 1976–2001

| | | 1976 | 1977 | 1978 | 1979 | 1984 | 1985 | 1986 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Sampling dates** | Initial | 21/7 | 9/7 | 5/7 | 1/7 | 9 | 15 | 12 | 15/6 | 14/6 | 15/6 | 15/6 | 15/6 | 16/6 | 15/6 | 14/6 |
| | Final | 22/8 | 1/9 | 18/8 | 23/8 | 28/7 | 24/7 | 21/7 | 4/8 | 14/8 | 17/8 | 10/8 | 10/8 | 19/8 | 11/8 | 12/8 |
| **Total n** | | 47 | 95 | 131 | 81 | 32 | 13 | 55 | 85 | 118 | 107 | 90 | 88 | 86 | 83 | 93 |
| **Fish** | | | | | | | | | | | | | | | | |
| Ammodytidae | | | | | | | | | | | | | | | | |
| Sand lance *Ammodytes hexapterus* | | 3.7 | 45.4 | 6.7 | 67.0 | 12.2 | 85.6 | 46.1 | 47.4 | 31.2 | 23.5 | 16.3 | 24.9 | 61.1 | 51.8 | 49.9 |
| Scomberesocidae | | | | | | | | | | | | | | | | |
| Pacific saury *Cololabis saira* | | 90.7 | 44.7 | 19.8 | 29.6 | 25.9 | 2.7 | 26.5 | 27.8 | 3.1 | 3.2 | 31.3 | | 16.1 | 3.7 | 37.9 |
| Scorpaenidae | | | | | | | | | | | | | | | | |
| Rockfish *Sebastes* spp. | | | 3.4 | 13.6 | 2.6 | 56.7 | 7.8 | 13.4 | 12.2 | 23.1 | 7.2 | 24.7 | 30.1 | 12.0 | 26.4 | 1.0 |
| Clupeidae | | | | | | | | | | | | | | | | |
| Pacific herring *Clupea pallasi* | | 1.8 | 1.1 | 0.3 | 0.7 | | | | 1.1 | 11.4 | 45.2 | 0.3 | 36.0 | 3.9 | | |
| Argentinidae | | | | | | | | | | | | | | | | |
| Blue-throat argentine *Nansenia candida* | | | | 52.9 | | | | | | | | | 0.4 | | | |
| Salmonidae | | | | | | | | | | | | | | | | |
| Salmon *Oncorhynchus* spp. | | 3.5 | 0.9 | 0.9 | | | | 8.5 | 1.1 | 18.7 | 14.0 | 9.2 | 7.7 | 1.9 | 15.3 | 6.7 |
| Hexagrammidae | | | | | | | | | | | | | | | | |
| Kelp greenling *Hexagrammos decagrammus* | | | | 1.0 | | 1.2 | 2.0 | 4.5 | 6.6 | 6.1 | 3.4 | 0.7 | 0.4 | 1.1 | 0.3 | 0.6 |
| Anoplopomatidae | | | | | | | | | | | | | | | | |
| Sablefish *Anoplopoma fimbria* | | | 4.4 | 4.1 | | 0.5 | | | 0.9 | 1.6 | 0.1 | 2.3 | 0.2 | 2.7 | 1.2 | 1.2 |
| Gadidae | | | | | | | | | | | | | | | | |
| Pacific hake *Merluccius productus* | | | | | | | | | | | | 12.7 | | | | |
| Walleye pollock *Theragra chalcogramma* | | | | | | | | | | 1.2 | | | | | | |
| Unidentified gadid | | | | | | | | | | | 0.0 | | | 0.1 | | |
| Agonidae | | | | | | | | | | | | | | | | |
| Northern spearnose poacher *Agonopsis emmelane* | | | | | | | | | | 0.1 | | | | | | |
| Cottidae | | | | | | | | | | | | | | | | |
| Cabezon *Scorpaenichthys marmoratus* | | | 0.0 | | | | | | | 0.5 | 0.0 | 0.1 | | | | |
| Pleuronectidae | | | | | | | | | | | | | | | | |
| Unidentified flatfish | | | | | | | | 0.0 | 0.0 | 0.1 | | | | | | |
| Paralepididae | | | | | | | | | | | | | | | | |
| Slender barracudina *Lestidium ringens* | | | | 0.1 | | 0.9 | | | 0.1 | 0.7 | | 0.6 | | | 0.3 | |
| Zaproridae | | | | | | | | | | | | | | | | |
| Prowfish *Zaprora silenus* | | | | | | | | | | 0.2 | | | | | | |
| Anarhichadidae | | | | | | | | | | | | | | | | |
| Wolf eel *Anarrhichthys ocellatus* | | | | | | | | | | 0.2 | | | | | | |
| Unidentified fish | | 0.2 | | | | 1.6 | | | 0.2 | 0.2 | 1.1 | | | 1.2 | 0.1 | 1.2 |
| **Cephalopods** | | | | | | | | | | | | | | | | |
| Unidentified squids | | | | 0.5 | 0.1 | 1.1 | 1.9 | 1.0 | 2.5 | 1.8 | 2.4 | 1.9 | 0.1 | 0.0 | 0.9 | 1.5 |
| **Total number prey** | | 98 | 690 | 639 | 540 | 241 | 260 | 315 | 950 | 640 | 496 | 662 | 483 | 750 | 586 | 556 |
| **Total wet mass (g)** | | 1713 | 2851.6 | 3919.9 | 1755.5 | 774.3 | 450.1 | 1712.6 | 2277.9 | 2889.8 | 2499.3 | 2327.2 | 2098 | 1919.1 | 2023.3 | 2474.2 |

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