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

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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.

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

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

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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

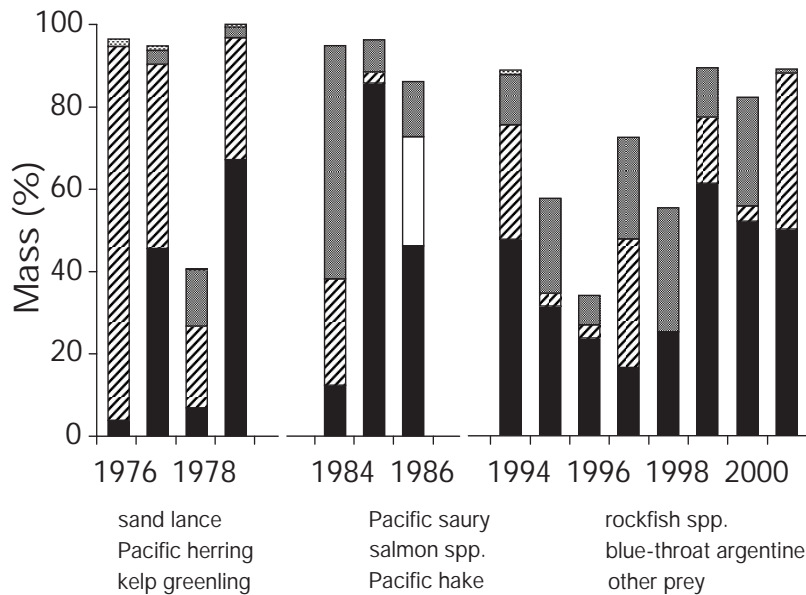1204 food samples (total mass = 29 408 g) were collected between 1976 and 2001 (Appendix 1). Bill loads averaged 26.4 ± 0.4 g (range = 0.7 to 85 g, n = 1189) and contained 6.4 ± 0.2 prey items (range = 1 to 36, n = 1191). While bill loads collected in July were largely similar in size across years, those 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) 0+,1+	8.6 ± 0.4 (289)	24.3 ± 0.7 (289)	130	Vermeer & Westrheim (1984)
Pacific saury	167 ± 1.7 (298) 0+	2.0 ± 0.1 (174)	34.8 ± 0.9 (174)	145	Suyama et al. (1996)
Rockfish spp.	60 ± 0.2 (1871) 0+	7.1 ± 0.3 (139)	17.6 ± 0.7 (139)	79	Phillips (1964), Westrheim & Harling (1975)
Pacific herring	129 ± 3.1 (105) 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) 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 p < 0.001	$F_{5,733}$ = 44.67 p < 0.001		

sand lance
Pacific herring
kelp greenling

Pacific saury
salmon spp.
Pacific hake

rockfish spp.
blue-throat argentine
other prey

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

>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).

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

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

accounted for only 36% of the annual variation of
Pacific saury in chick diet (Fig. 7A), this species was all

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

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:

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

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

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

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

July dietary measures:

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

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

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

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

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 SGaang 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

dent stock assessment, as the 1994 year class was the

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

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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		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**																