Short visits reveal consistent patterns of interyear and intercolony variation in seabird nestling diet and performance

D.F. Bertram, T. Golumbia, G.K. Davoren, A. Harfenist, and J. Brown

Abstract: To investigate the utility of short visits to seabird colonies to gauge nestling growth performance and diet, in 4 consecutive years (1995–1998) we measured nestling development and diet of Rhinoceros Auklets (*Cerorhinca monocerata*) at three colonies in British Columbia: Seabird Rocks, Triangle Island, and SGaang Gwaii (Anthony Island). In all years, nestlings of a given wing length on Triangle Island were significantly smaller than those on Seabird Rocks or SGaang Gwaii. Meals were also significantly lighter on Triangle Island than on Seabird Rocks or SGaang Gwaii; meals on the latter two islands were indistinguishable in mass. Retarded nestling development and small meal size on Triangle Island likely reflect the large contribution of rockfish (*Sebastes* spp.) to nestling diet on that colony alone. The intercolony differences in nestling performance appear to reflect the strong influence of local fish prey populations. Nonetheless, a united decline in performance in 1996 and subsequent increase on all colonies suggest the influence of large-scale ocean climate phenomena on our entire study region and beyond. We did not, however, observe noticeable effects of the 1997–1998 El Niño Southern Oscillation event on nestling growth performance or diet. We discuss the utility of our short-visit techniques for seabird-monitoring programs.

Résumé : Nous avons évalué l'efficacité de courtes visites à une colonie d'oiseaux marins pour mesurer la performance de croissance et le régime alimentaire d'oisillons au nid. Durant 4 années consécutives (1995–1998), nous avons mesuré le développement et le régime alimentaire de petits macareux rhinocéros (*Cerorhinca monocerata*) au nid dans trois colonies de Colombie-Britannique : Seabird Rocks, Triangle Island et SGaang Gwaii. Tous les ans, les petits macareux d'une longueur d'aile donnée sont significativement plus petits sur Triangle Island que sur Seabird Rocks ou SGaang Gwaii et la masse de leurs repas y est aussi plus faible que sur les deux autres îles où les masses alimentaires sont semblables. Le développement retardé des oisillons au nid à Triangle Island et leurs repas réduits reflètent sans doute l'importante proportion de sébastes (*Sebastes* spp.) à l'alimentation des petits macareux, ce qui ne se produit pas dans les autres colonies. Les différences de performance des oisillons au nid dans les différentes colonies semblent être le reflet de l'influence des populations locales de poissons proies. Néanmoins, un déclin de la performance s'est produit dans toutes les colonies en 1996, suivi d'un regain général; cela laisse croire à l'influence d'un phénomène climatique océanique à grande échelle qui a affecté toute la région de l'étude et au-delà. Nous n'avons cependant pas observé d'effets mesurables du phénomène d'El Niño de 1997–1998 sur la performance de croissance ou sur le régime alimentaire des petits macareux au nid. L'utilité de notre technique de visites courtes dans le cadre de programmes de surveillance des oiseaux marins fait l'objet d'une discussion.

[Traduit par la Rédaction]

Introduction

In investigations of marine ecosystems, seabirds can be used to provide unique samples from the environment that supply information on both seabirds and prey populations. Measurements of seabird nestlings coupled with samples of nestling diet can provide general insight into relationships between developmental performance and local marine prey

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species composition. At larger spatial scales, intercolony time-series comparisons can also provide insight into recruitment to prey populations (e.g., Bertram and Kaiser 1993). In addition, seabird-nestling diets often represent the only regional samples of fish species and thus may provide the sole data on some prey populations, particularly at the juvenile stages (Cairns 1987, 1992; Montevecchi 1993).

Canada has an estimated 56% of the world's population of Rhinoceros Auklets (*Cerorhinca monocerata*) at several important breeding colonies in British Columbia (Rodway 1991), and hence has significant international stewardship and conservation responsibilities for the species. Moreover, for conservation actions, it is necessary to have current time series on reproductive performance and prey populations that can be used to examine natural variation and help gauge the impacts of human-induced perturbations, such as oil pollution or fishery interactions (e.g., Furness and Tasker 2000; Montevecchi 2002). An important consideration for the design of cost-effective monitoring programs that we address here is the duration of a visit to the seabird colony.

Boyd and Murray (2001) recently demonstrated that upper trophic level predator responses could be used to monitor the marine ecosystem at South Georgia in the Antarctic Ocean. Moreover, they showed that variables representing offspring growth tend to explain the greatest proportion of the variability in a combined standardized index (based upon up to 27 variables measured over 22 years) followed by variables representing diet. In the present study, we measure nestling growth and diet during short visits (or restricted time frames) to investigate the utility of the methods used for monitoring seabird production.

We measured the developmental performance and diet of Rhinoceros Auklet nestlings annually for 4 years at three widely separated colonies in British Columbia. We sought to identify spatial and temporal patterns within the scale of our examination. We asked three main questions: Are there differences in nestling growth performance and diet between colonies? What is the relationship between nestling growth performance and diet? Are there detectable dominant interannual effects that are observed at all colonies, and if so, do they indicate larger scale oceanographic phenomena such as El Niño Southern Oscillation (ENSO) events?

We discuss the utility and limitations of our approach, which is based on short visits to colonies for ecosystem-conservation and -monitoring programs and provide recommendations for future efforts.

Methods

Study sites

We conducted our investigation on three islands along the coast of British Columbia (Fig. 1). The southernmost colony, Seabird Rocks (48°45′N, 125°09′W), supports approximately 130–170 breeding pairs of Rhinoceros Auklets (Rodway 1991, Burger et al. 1993). Triangle Island (51°52′N, 129°05′W), the outermost island of the Scott Island chain, is by far the largest seabird colony in British Columbia, with 13 species, including an estimated 41 700 breeding pairs of Rhinoceros Auklets (Rodway et al. 1990b). The most northerly colony, SGaang Gwaii (52°05′N, 131°13′W; formerly Anthony Island), supports 13 800 pairs of breeding Rhinoceros Auklets

(Rodway et al. 1990a). We followed the same methodologies on all islands.

Nestling mass and wing length

We excavated burrows by digging access holes through the roof of the burrow tunnels until the nestling was accessible; between visits we covered access holes with cedar shingles and soil. We measured nestling mass to the nearest 2 g on spring scales and measured wing length, from the wrist to the tip of the flattened wing, to the nearest millimetre using a wing ruler. Nestlings were then returned to their burrows and not disturbed again until 10 d later, at which time we weighed and measured them again.

Nestling diet

We collected food from provisioning parents flying into the colonies. These collections were made close to the time of each of the two chick-measuring sessions and were done in a separate part of the colony to avoid interference. We intercepted adults flying into the colony with bill loads of fish and (or) squid by shining lights on the birds, making loud noises, or trapping the birds with a landing net. The adult usually dropped its load and we collected each load in a separate plastic bag. We used only those samples that we were certain constituted the full "bill load". On Seabird Rocks we also used "screens" placed at the burrow mouth that prevented incoming parents from entering and caused them to drop the food at the barrier. On the morning following collection, each bill load was weighed to the nearest 0.5 g. We identified and measured individual fish (standard length and mass) within each load and preserved the unknown fish for subsequent identification by an expert.

Statistical treatment

Mass versus wing length comparisons

On Triangle Island, researchers measured nestlings 3 or 4 times at 10-d intervals throughout the rearing period. Because the present study was carried out by distinct, cooperating research organizations at widely separated sites along the coast where timing of breeding varied, the ages of nestlings often differed between colonies at the time of measurement. However, by measuring nestlings on two occasions separated by 10 d, we had the opportunity to maximize comparability by selecting the dates that provided the greatest overlap of wing-length data between years and colonies. A single visit to Seabird Rocks in 1998 limited the selection process for comparable dates. The unit of measurement was individual bird mass in relation to wing length on the selected date, which can be thought of as "developmental space" or as representing a "developmental condition" index. We did not compare growth rates of individuals by examining mass gain during the 10-d interval because nestlings on some colonies were older and were reaching asymptotic sizes or even exhibiting mass loss as fledging approached. Note, too, that the dates used for mass verus wing comparisons were those obtained prior to exhibition of prefledging mass loss.

We compared the homogeneity of slopes of the mass versus wing length relationships by inspecting the significance of the interaction term in an analysis of covariance (ANCOVA) (i.e., mass = constant + wing + colony + wing × colony). If signifi-

Fig. 1. Locations of the Rhinoceros Auklet (*Cerorhinca monocerata*) colonies in the study. Note that SG̱aang Gwaii is also known as Anthony Island.
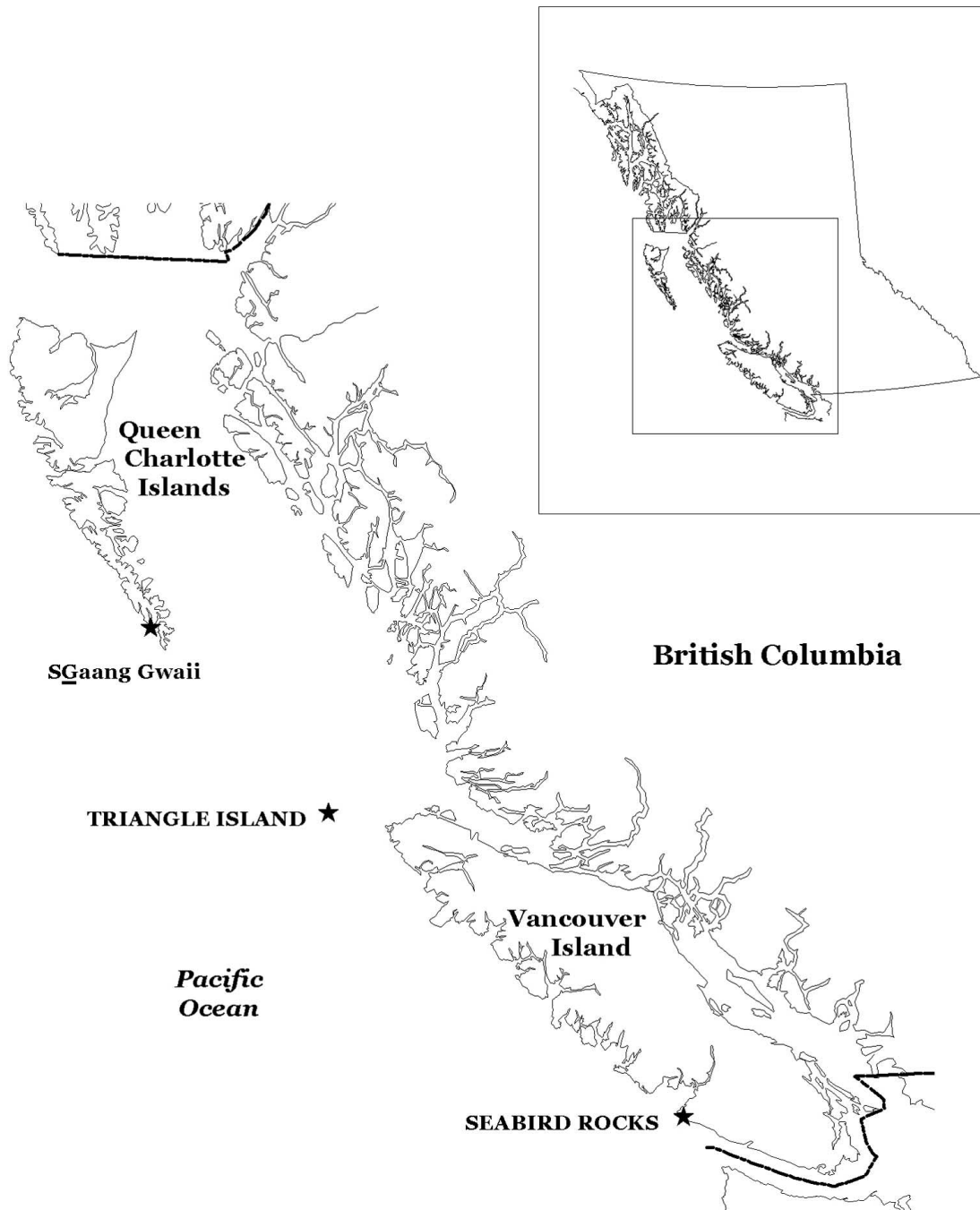
cant differences were found, multiple paired tests of colony or year were conducted to identify the steepest and shallowest slopes. We tested for differences in the elevation of the mass versus wing length relationship using the same model with retention of the interaction term in all cases. The ANCOVA adjusts the mean masses to compare them at the same wing length. Post-hoc contrasts were performed on the adjusted mean masses and significance was based on Bonferroni-adjusted probabilities.

Nestling diet

We compared the species composition of fishes in the nestling diet by pooling the bill loads collected within each year on each colony to obtain the percentage of mass composed of sand lance (*Ammodytes hexapterus*), Pacific herring (*Clupea pallasi*), rockfishes (*Sebastes* spp.), salmon (*Salmonid* spp.), surf smelt (*Hypomesus pretiosus*), Pacific saury (*Cololabis saira*), and Pacific hake (*Merluccius productus*). The percentages were arcsine and square-root transformed to investigate the differences between colonies for each species using a univariate ANOVA followed by post-hoc contrasts with Bonferroni-adjusted probabilities. The masses of food loads were compared between colonies by pooling all the loads collected within each year in a one-way ANOVA

followed by post-hoc contrasts with Bonferroni-adjusted probabilities.

Results

Nestling growth and developmental patterns

Intercolony comparisons

There were significant differences between colonies that persisted in all years of the study. Nestlings on Triangle Island had a significantly smaller mass for a given wing length than birds on either Seabird Rocks or SGaang Gwaii (Fig. 2, Table 1). In contrast, nestling development on Seabird Rocks and SGaang Gwaii was very similar except in 1998, when nestlings on SGaang Gwaii were significantly heavier than the nestlings on Seabird Rocks (Fig. 2, Table 2). The slopes of the relationship between mass and wing length tended to be less steep on Triangle Island than on the other colonies, which had similar values. When annual values for each colony were pooled, the mean slopes and elevations were lower on Triangle Island than on either SGaang Gwaii or Seabird Rocks, based on Bonferroni-adjusted comparisons of the mean values reported in Table 2. Note that the lowest values for slope and elevation on SGaang Gwaii were higher than the maximum values observed on Triangle Island (Table 2).

Interyear comparisons

Nestling development differed significantly between years on all colonies. All colonies tended to exhibit the poorest nestling developmental performance in 1996 (Fig. 3, Table 2). Within colonies, the slopes of the relationship between mass and wing length by date were statistically indistinguishable between years (Table 2), except on SGaang Gwaii in 1996 and 1997, when the lowest values were detected. Performance tended to improve on all colonies in 1997 and 1998 and some of the highest values for both slope and elevation estimates were observed in those years (Table 2).

Nestling diet

Species composition

Fish-species composition in nestling diets differed significantly and consistently between colonies and several major patterns are apparent (Fig. 4). Rockfishes composed a significantly greater proportion ($F_{[2,9]} = 11.6$, $P = 0.003$) of the nestling diet on Triangle Island (23%) than on SGaang Gwaii (7%) or Seabird Rocks (0%), where rockfishes were rarely observed. Percent composition of sand lance was significantly greater on SGaang Gwaii (74% in 1995–1998) than on either Seabird Rocks (20%) or Triangle Island (6%), which had similar values ($F_{[2,9]} = 27.1$, $P < 0.001$; post-hoc contrasts are Bonferroni-adjusted probabilities). We could not detect a statistical difference ($F_{[2,9]} = 0.47$, $P = 0.64$) between the percentages of herring on Seabird Rocks (16%) Triangle Island (33%), and SGaang Gwaii (14%). Salmonid representation in the mass of bill loads was statistically indistinguishable on Seabird Rocks (32%) and Triangle Island (14%), and both exceeded SGaang Gwaii (2%), where salmon were rare ($F_{[2,9]} = 9.8$, $P = 0.005$). Surf smelt formed a significant part of the nestling diet on Seabird Rocks in 3 of the 4 years (47% in 1995; 20% in 1996;0 in 1997; 48% in 1998) but were absent from the other colonies. In 1997, Pa-

cific saury (39%) and Pacific hake (21%) were found on Triangle Island but did not occur elsewhere. On all colonies, no single species dominated the diets within any given year of our study.

Bill-load size

Bill-load masses were significantly lower on Triangle Island than on Seabird Rocks or SGaang Gwaii (Table 3). The mean masses of bill loads ranged widely, from 20.3 g on Triangle Island to 44.1 g on Seabird Rocks.

Discussion

The consistency of the pattern of smaller nestling mass in relation to wing length on Triangle Island in all 4 years of the study is marked. In addition, in most years we could not detect a difference in nestlings' mass versus wing length values between Seabird Rocks and SGaang Gwaii. In 1998, however, nestlings on Seabird Rocks and SGaang Gwaii differed from each other in mass versus wing length values, though we could not detect significant differences between nestlings on Seabird Rocks and Triangle Island despite the persistent trend for the lowest values to be observed on Triangle Island. The anomalous result in 1998 was probably due to the fact that Seabird Rocks was visited only once that year and the overlap in wing lengths between colonies was constrained, thus limiting our comparison (see below). In addition to differences in elevation, we also observed a tendency (significant in 1995 and 1998) for the slope of the mass versus wing length relationship to be lower on Triangle Island than on the other colonies. The differences in the slopes of the bivariate (mass versus wing length) plots suggest that nestlings on Triangle Island followed a different developmental trajectory than nestlings on the other colonies. Our results suggest that the differences in development stemmed largely from lower food quantity and perhaps quality (see below) on Triangle Island. It is known that when food intake by Atlantic puffins (*Fratercula arctica*) is reduced, growth of both mass and wing length is depressed, but also wing length grows preferentially relative to mass (Øyan and Anker-Nilssen 1996). Thus, it is likely that the developmental trajectory of the nestlings on Triangle Island represented the outcome of slower mass and wing growth subject to preferential growth of the wing. Below we discuss further reasons for the striking intercolony differences, investigate causes of the patterns of variation between years, and evaluate the utility of our methods of monitoring to support management and marine conservation efforts.

Intercolony variation

Variation in the prey-species composition of nestling diets is central to the observed differences in nestling-development patterns between colonies. Rockfish composed a significant part of nestling diets at Triangle Island, where nestling development was retarded, compared with the other colonies, where rockfish were rare. Bertram and Kaiser (1993) also observed slower nestling growth rates on Rhinoceros Auklet colonies (Triangle Island and Pine Island (50°35′N, 127°26′W)) where rockfish composed large proportions of the diet. Those authors showed that bill loads composed only of rockfish were significantly lighter than the sand lance loads and the two species are reported to have similar caloric

Fig. 2. Intercolony variation in nestling development in 1995, 1996, 1997, and 1998. Each ellipse is centered around the mean for the corresponding colony and encompasses 60% of the individual values obtained on the day of measurement. SBR, Seabird Rocks; TRI, Triangle Island; SG, SGaang Gwaii.
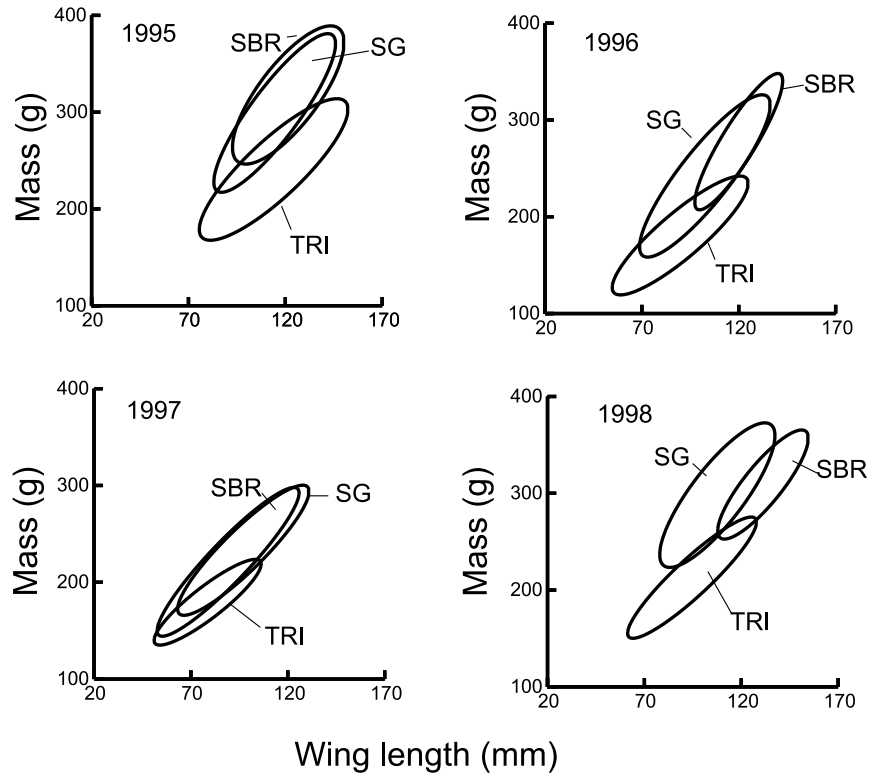

Table 1. Summary statistics for comparisons between Rhinoceros Auklet (*Cerorhinca monocerata*) colonies, using ANCOVA for homogeneity of slope (wing × year) followed by tests of elevation (mass versus wing length).

Year	Colony[a]	Date in July	n[b]	Slope[c] of mass versus wing length bivariate relationship (g·mm^{-1})	Elevation (ALS mean mass versus wing length)[d]
1995	SBR	15	11	1.88*ab*	309*a*
	TRI	18	33	1.68*b*	246*b*
	SG	20	43	2.34*a*	311*a*
1996	SBR	17	12	2.18*a*	236*a*
	TRI	17	24	1.53*a*	196*b*
	SG	22	44	2.17*a*	237*a*
1997	SBR	12	12	1.94*a*	220*a*
	TRI	14	37	1.43*a*	194*b*
	SG	17	43	1.79*a*	218*a*
1998	SBR	21	16	2.05*ab*	256*b*
	TRI	13	39	1.73*b*	231*b*
	SG	16	58	2.41*a*	295*a*

Note: Post-hoc contrasts (*a* and *b*) indicate similarities and differences.

[a]SBR, Seabird Rocks; TRI, Triangle Island; SG, SGaang Gwaii.

[b]Number of nestlings measured.

[c]If differences were detected, post-hoc contrasts on slopes were based on multiple paired comparisons.

[d]Adjusted least square (ALS) means based upon the ANCOVA including the interaction term. Tests of mean elevations of mass versus wing length were conducted using Bonferroni-adjusted probabilities of post-hoc contrasts.

values (Vermeer and Devito 1986). In the present study, bill loads were again lighter on Triangle Island. We consider the lighter loads on Triangle Island to reflect the dominant rock-

fish composition and suggest that the bill-load size is constrained by the squat body morphology of the rockfish prey. Nestling age has been shown to affect the amount of food

Table 2. Summary statistics for interyear comparisons using ANCOVA for homogeneity of slope (wing × year) followed by tests of elevation (mass versus wing length).

Colony	Year	n^a	Slope[b] of mass versus wing length bivariate relationship (g·mm^{-1})	Elevation (ALS mean mass versus wing length)[c]
SBR	1995	11	1.88a	305a
	1996	12	2.18a	267b
	1997	12	1.94a	271a
	1998	16	2.05a	275a
	All	4	2.01	279.5
TRI	1995	33	1.62a	209a
	1996	24	1.53a	187b
	1997	37	1.43a	202a
	1998	39	1.73a	212a
	All	4	1.58	202.5
SG	1995	43	2.35a	282a
	1996	44	2.18 ab	249b
	1997	43	1.79b	249b
	1998	58	2.41a	296a
	All	4	2.18	269

Note: For names of colonies and sampling dates see Table 1.

[a]Number of nestlings measured.

[b]If differences were detected, post-hoc contrasts on slopes were based on multiple paired comparisons.

[c]Adjusted least square (ALS) means based upon the ANCOVA including the interaction term. Tests of mean elevations of mass versus wing length were conducted using Bonferroni-adjusted probabilities of post-hoc contrasts.

delivered to the burrow (e.g., Bertram et al. 1991), but there was considerable overlap in nestling-developmental stages between colonies.

Sand lance consistently composed most of the nestling diet on SGaang Gwaii, where nestling growth performance was strong. Rapid nestling development (e.g., measured in grams per day) has been associated with high proportions of sand lance in the diet (Wilson and Manuwal 1986; Bertram and Kaiser 1993). The present study also demonstrates strong nestling performance on diets that were not exclusively dominated by sand lance. Nestlings on Seabird Rocks performed as well as those on SGaang Gwaii on varied diets composed of surf smelt, herring, and salmon in addition to sand lance. Bill-load masses were similarly large on Seabird Rocks and SGaang Gwaii and the diet on Seabird Rocks routinely included surf smelt and herring, which have a similar energy density to sand lance (e.g., for data from Alaska see Anthony et al. 2000). On Teuri Island in Japan (44°25′N, 141°19′E), Rhinoceros Auklet nestlings grew most rapidly and fledged at heavier masses when provisioned primarily with anchovy (*Engraulis japonicus*) because bill loads were heavier and energy densities were higher than those reported for 0+ sand lance (Takahashi et al. 2001). Clearly, regional differences in nestling performance will depend on the regional availability of alternative prey species and the age classes present within the breeding season.
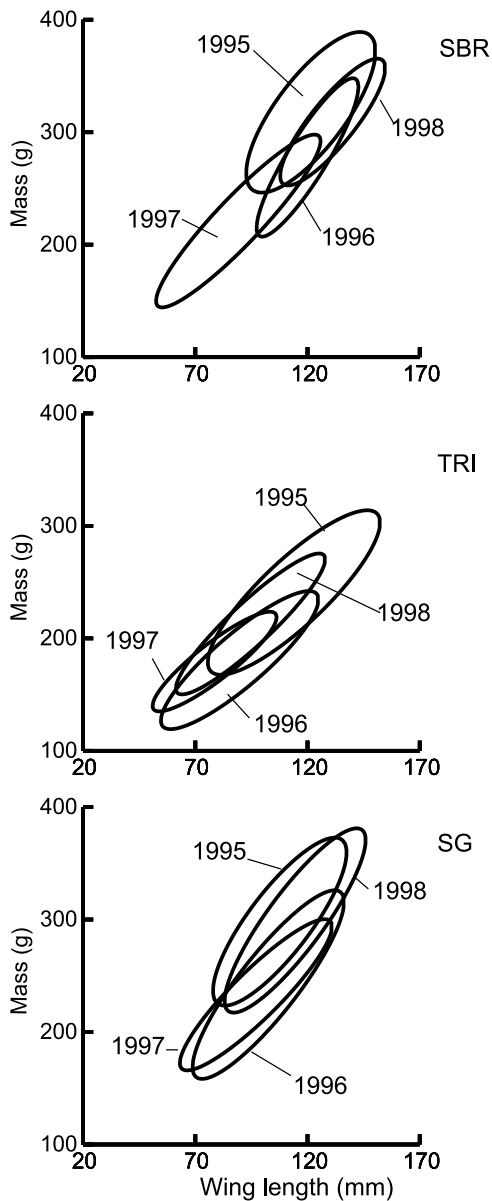
Ocean temperatures on the British Columbia coast dropped significantly in 1999 to levels that were observed in the 1970s and have remained low, in contrast to those reported for most of the 1990s. On Triangle Island, sand lance abundance in the diets of Rhinoceros Auklet nestlings increased, to exceed 50% by mass in 1999, and nestling growth rates also exhibited a marked increase in that year compared with those found in this study (1995–1998), when rockfish and other species were dominant (Bertram et al. 2001; Department of Fisheries and Oceans 2001). It is plausible that re-

cruitment to sand lance populations around Triangle Island increases in cool years (Bertram et al. 2001) such as 1999, but independent data on prey abundance are needed to test this hypothesis. Our results herein (1995–1998) demonstrate that when sand lance did not dominate nestling diets on Triangle Island, growth rates on the alternative prey species were relatively poor.
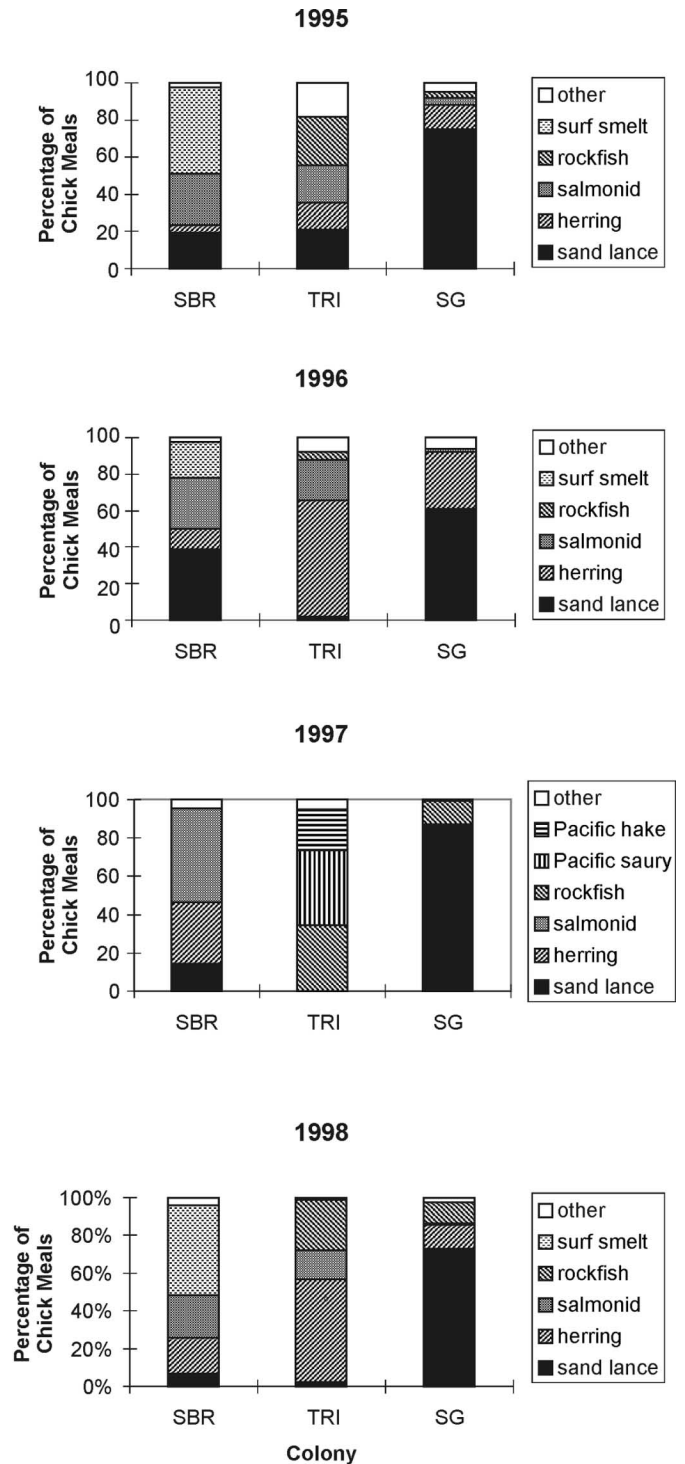
Interyear variation

Between years, colonies generally tended to show similar rankings in nestling performance, rising and falling in unison. Most notably, nestlings on all colonies tended to perform poorest in 1996. The interyear similarity in performance on the widely separated colonies suggests the presence of oceanographic influences that operate at a larger spatial scale than in our study area. In a recent study, Whitney et al. (1998) argued that "there are interannual changes in seawater properties in the NE Pacific Ocean which affect nutrient supply and primary production, and by inference, higher trophic level productivity". Estimates of nitrate depletion in a 290 000-km^2 patch off the west coast of Vancouver Island from 1989 to 1996 were lowest in 1996, consequently new production was reduced by 40% through spring and summer. Whitney et al. (1998) argued that observed variability in mixed-layer water properties (such as nitrate) in the northeast Pacific Ocean is not regional but results from changes in atmospheric forcing that likely affect the entire North Pacific Ocean. The mechanisms leading to a reduction in seabird performance at basin-level scales are presently unclear and are likely to affect different species in different ways. During the study period the water temperatures in British Columbia were among the highest of the century, and spring was early, particularly in 1996 and 1998. In those early, warm spring years, production of Cassin's Auklet nestlings on Triangle Island was exceedingly poor, likely because of a mismatch in timing between the availability of the principal copepod prey (*Neocalanus cristatus*)

Fig. 3. Interyear variation (1995–1998) in nestling development on Seabird Rocks (SBR), Triangle Island (TRI), and SGaang Gwaii (SG). Each ellipse is centered around the mean for the corresponding year and encompasses 60% of the individual values obtained on the day of measurement.

Fig. 4. Prey species composition in nestling diets (percent wet mass) on Seabird Rocks (SBR), Triangle Island (TRI), and SGaang Gwaii in 1995, 1996, 1997, and 1998.

and seabird breeding (Bertram et al. 2001). The copepod prey disappeared early from surface waters (and hence from nestling diets) in 1996 and 1998, and as a consequence the Cassin's Auklet (*Ptchoramphus aleuticus*) nestlings grew slowly and many starved. We expect that because zooplankton prey populations have annual life cycles and can exhibit massive community species reorganization from one year to the next (see Mackas et al. 2001), variation in reproductive performance of the largely planktivorous Cassin's Auklet should closely track variability in zooplankton prey populations. For the largely piscivorous Rhinoceros Auklet, however, we expect that because of the addition of another trophic level that consists of age-structured prey populations, the connection between ocean forcing and seabird reproductive performance will be-

come less direct and thus more complicated. Nonetheless, it is striking that despite differences in trophic level between species, 1996 was uniformly the poorest year for nestling performance during the 1990s for Rhinoceros Auklet, Tufted Puffin (*Fratercula cirrhata*), and Cassin's Auklet populations on Triangle Island (Bertram et al. 2001). The trophic connectivity between zooplankton prey populations, pelagic fish preda-

Table 3. Summary of bill loads delivered to Rhinoceros Auklet nestlings by colony, year, and date.

Colony	Year	Sampling date(s) in July 1	2	Mean bill-load mass (g) 1	2	No. of bill loads 1	2	Colony mean mass Mean	SE	Post-hoc contrast[a]
SBR	1995	4, 5	14–16	39.3	27.6	7	13	35.8	1.86	*a*
	1996	7, 9	17, 18	33	33.7	16	15			
	1997	2	12	34.6	38.3	8	9			
	1998	21		44.4		12				
TRI	1995	10	25	21.1	23.7	12	19	27.3	1.7	*b*
	1996	12	19	31.6	29.2	17	9			
	1997	13	20	30.7	31.8	10	10			
	1998	20	25, 27	20.3	29.9	10	11			
SG	1995	20	30	41.7	32.6	36	36	34.9	1.7	*a*
	1996	20	30	31.3	34.4	36	35			
	1997	15,16	25, 26	27.1	36.2	37	36			
	1998	16	26	39.4	36.7	37	36			

Note: For names of colonies and sampling dates see Table 1.

[a]Based upon Bonferroni-adjusted probabilities.

tors (including seabird prey such as sand lance, herring, salmon, and rockfish), and breeding piscivorous seabirds such as the Rhinoceros Auklet is an open research topic that requires an integrated, ecosystem-based investigative approach.

It is important to point out that our study did not detect any major influences on nestling performance or diet in 1998, when a very large ENSO event was observed (PICES 1999). In 1998, values for nestling performance on all colonies ranked among the highest observed. (Note that the highest values observed on Triangle Island were still lower than all of those measured on the other colonies.) We do not suggest, however, that the ENSO event had no effect on seabirds in British Columbia. The number of birds attempting to breed (based upon burrow occupancy) was significantly reduced for the Cassin's Auklets on both Triangle Island and Frederick Island (53°56′N, 133°11′W), although poor nestling performance was only observed on Triangle Island (Bertram et al. 2001; A. Harfenist, personal observation). Time-series information (1983–1999) for Ancient Murrelets (*Synthliboramphus antiquus*) from the Queen Charlotte Islands indicate that the 1998 ENSO event significantly reduced breeding success, resulting in an average of <1 chick reared per breeding pair compared with average values of >1.4 chicks per pair (Gaston and Smith 2001).

The present study reports only on nestling development and diet and does not offer information on parental foraging effort such as regularity of feeding or distance traveled to the feeding areas from the colony. It is known that breeding Rhinoceros Auklets (Bertram et al. 1996), like many other seabirds (Ydenberg and Bertram 1989; Burger and Piatt 1990; Monaghan et al. 1994; Shaffer et al. 2001; Hedd et al. 2002), can adjust parental provisioning effort. Consequently, within certain levels of prey availability, seabirds have a buffering capacity and may mask the effects of poor ocean foraging conditions on nestling growth by increasing their provisioning effort. Nonetheless, because the Rhinoceros Auklet is a nocturnal single-load-provisioning species, its potential to buffer environmental vagaries may be constrained (Takahashi et al. 1999) compared with other, multiload-provisioning species. We were not able to evaluate the effects of population and colony size (e.g., Hunt et al. 1986) on performance, owing to the lack of replicate colonies.

Utility of methods for marine-ecosystem monitoring

Our monitoring technique, based on short visits to seabird colonies, is attractive to marine management and conservation programs because it provides valuable insight into both seabird and prey fish populations at a low cost and with minimal disturbance. To be most effective, future visits to colonies should be timed so that nestlings are at comparable stages of development, prior to the onset of prefledging mass loss. Because of constraints on the timing of our visits to SGaang Gwaii and Seabird Rocks, nestlings on different colonies were at different stages of development. (Note that our short-visit method precluded reliable estimates of hatch dates from back-calculations of wing-length measurements because most of our measurements were taken relatively late in development and wing length is known to become a progressively poorer predictor of age as the wings become longer. In addition, it is known that the wing-length growth rate in captive Atlantic Puffins is influenced by diet (Øyan and Anker-Nilssen 1996), but we lack similar studies of the Rhinoceros Auklet that could be used to correct for diet-induced variation in the relationship between wing length and age.) In 1998, Seabird Rocks was visited only once and no differences between Triangle Island and Seabird Rocks could be detected in our intercolony comparisons for that year, unlike all previous years. However, when we repeated the analysis with selected dates for Triangle Island and SGaang Gwaii that were 10 d later, nestling performance was significantly poorer on Triangle Island than on Seabird Rocks and SGaang Gwaii, as observed in all other years.

The methods outlined here do not provide information on breeding propensity, parental provisioning effort, seasonal changes in diet, or population trends. Clearly, methods based upon short visits to colonies cannot replace detailed integrated investigations for gaining mechanistic insights into the response of upper trophic levels to variation in marine ecosystems. Nonetheless, the subset of results presented here for Triangle Island based upon cross-sectional data (Case 1978) is consistent with the patterns observed when more extensive longitudinal growth datasets are examined (e.g., Bertram et al. 2001; Triangle Island Research Station, unpublished data). Nestling growth rates (from 10 to 40 d) averaged 4.7, 3.1, 4.4, and 4.6 g·d^{-1} in 1995, 1996, 1997 and

1998, respectively. Fledging masses were 299, 229, 224, and 255 g in 1995, 1996, 1997, and 1998, respectively. Fledging success (fledged/hatched) was 81, 53, 70, and 82% in 1995, 1996, 1997 and 1998, respectively. Most notably, the rankings of the growth-rate estimates and the mass versus wing length comparisons between years are the same for both methods, with 1996 falling below the other years. In general, 1996 stands out as the poorest year for performance, based upon both the longitudinal datasets and the cross-sectional data analyses of mass versus wing length. The cross-sectional data and the longitudinal growth data, however, cannot capture events that take place following the sampling periods, as exemplified by 1997. Both the longitudinal growth data and the cross-sectional data were similar in 1995, 1997, and 1998 and values were higher than in 1996, but at the end of the breeding season in 1997, fledging mass was the lowest observed and fledging success was also lower, making 1997 more similar to the poorest year, 1996. Time-series data from Triangle Island indicate that the years of the present study coincided with an extended period of below-average performance and considerable nestling mortality (Bertram et al. 2001), which helps to explain the consistently low ranking of nestlings on Triangle Island compared with the other colonies reported here. Note, too, that in contrast to that of the other populations, the consistently poor performance of nestlings on Triangle Island highlights the necessity for having multiple colonies with wide spatial separation for seabird-monitoring programs.

Ultimately, conservation programs require estimates of population trends. We suggest that short visits to seabird colonies can be combined with indexes of population size based on burrow counts (e.g., Lemon and Gaston 1999) and other methods such as radar monitoring (Bertram et al. 1999) to establish the time-series data required for investigating trends.

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