

# PATTERNS IN THE PROVISIONING AND GROWTH OF NESTLING RHINOCEROS AUKLETS

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**ABSTRACT.**—We studied (1983–1987) the provisioning and growth of nestling Rhinoceros Auklets (*Cerorhinca monocerata*) in a breeding colony on the Lucy Islands and measured growth (1984–1986) in other colonies also on the British Columbia coast (Pine Island and Triangle Island). There were strong differences in the pattern of provisioning among the three years. In 1985 provisioning peaked around the midpoint (30 days) of the nestling period and then declined rapidly. In 1986, provisioning also declined after the midpoint, but more slowly than in 1985. In 1987, provisioning remained approximately constant during the entire breeding season. We found no evidence that late-hatched chicks were consistently fed less than early-hatched chicks, though the statistical power of the tests made to detect this difference was low. There were significant annual differences in chick growth. Growth was fastest in 1985, intermediate in 1984 and 1986, and slowest in 1983 and 1987. The mean growth rate on the three colonies changed in unison from year to year. Hypotheses based on seasonal environmental changes and on systematic changes in the food requirements of growing chicks do not explain the observed patterns. Our data on chick growth and independent data on ocean production suggest that the two varied directly and in unison among years. However, provisioning in the latter part of chick development did not appear to reflect directly the quality of ocean feeding conditions. We conclude that although large-scale fluctuations in ocean production are likely to be the dominant influence upon provisioning, the manner in which parents respond to such variation is poorly understood. Received 3 January 1990, accepted 17 March 1991.

PARENTS of most seabird species provision their offspring with food collected at sea and delivered to the nest. Among the Alcidae this behavior has been described for many species and has been shown to change with a variety of factors, such as weather (Birkhead 1976, Hatch 1984), fish stocks (Harris 1978, Harris and Hislop 1978, Hislop and Harris 1983, Springer et al. 1984, Furness and Barrett 1985, Barrett et al. 1987, Baird 1990), the age of the chick (Harris and Hislop 1978, Ashcroft 1979, Hudson 1979), and position of the nest (Nettleship 1972, Harris 1984). The growth of the nestlings of many species was reviewed by Gaston (1985). Many investigators have measured provisioning and growth in successive years at the same colony (e.g. Ashcroft 1979, Vermeer 1979, Gaston and Nettleship 1981, Wehle 1983), but only a few studies have reported measurements of growth

and provisioning at a number of colonies collected over successive years (Harris 1978, Harris and Hislop 1978, Wilson and Manuwal 1986, Barrett et al. 1987). Barrett et al. (1987) showed that the breeding success of Atlantic Puffins (*Fratercula arctica* L.) was similar over large sections of the Norwegian coast. Colonies in the central area failed completely in three of the four study years, while those in the northern and southern regions had good breeding success. All the colonies enjoyed good breeding success in 1983. Barrett et al. (1987) linked these patterns to the level of herring (*Clupea harengus* Valenciennes) stocks. In Britain it was found that puffins on St. Kilda were short of the "best" prey species compared with those on the Isle of May and thus had difficulty rearing young (Harris 1978, Harris and Hislop 1978). We measured the growth and provisioning in the Rhinoceros Auklet (*Cerorhinca monocerata* Pallas) at three colonies on the British Columbia coast. We found that these measures changed greatly from year to year, and that the growth of nestlings changed in unison at these colonies. We examine three hypotheses to explain the observed patterns.

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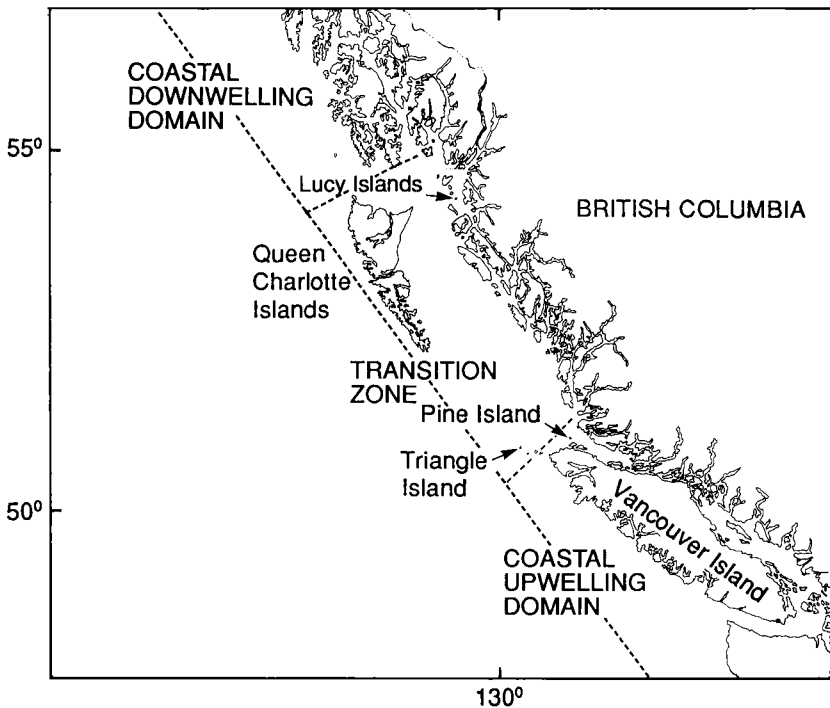


Fig. 1. Coastal British Columbia, showing Lucy Islands, Pine Island, and Triangle Island, the locations of the three study colonies. Oceanic features (terminology from Ware and McFarlane 1989) referred to in the text are also shown.

#### METHODS

Rhinoceros Auklets occur throughout the northern Pacific Ocean (Vermeer 1979). Their breeding biology and natural history have been documented (Richardson 1961, Leschner 1976, Wilson 1977, Summers and Drent 1979, Vermeer 1979, Hatch 1984, Wilson and Manuwal 1986). The single egg is laid in a burrow in late April or May, and incubated from 39 to 52 days (average 45 days). Parents feed their chicks at night (but see Thorenson 1983) and may remain on the colony during the dark hours, but they depart before sunrise. One or both parents may feed the chick each night during a single visit to the burrow, although Richardson (1961) reports instances of three visits to a single burrow in one night. On some nights neither parent may visit. A parent may deliver one large fish (up to 55 g, pers. obs.), or up to 20 smaller fish carried cross-wise in its bill. We refer to each such delivery as a "bill load." In British Columbia, Pacific sandlance (*Ammodytes hexapterus* Pallas) is the dominant prey species although herring and rockfish (*Sebastes* spp.) are also common prey (see Vermeer and Westrheim 1984).

The growth rate of Rhinoceros Auklet nestlings is among the slowest in the Alcidae (Ydenberg 1989). Chicks leave the nest at 50–80% (250–400 g) of adult weight (Vermeer and Cullen 1979; pers. obs.) at 45–

60 days of age, and are independent while they complete their development at sea after fledging. Rhinoceros Auklets from British Columbia probably winter off the California and Oregon coast (Kaiser et al. 1984).

*Study areas.*—The provisioning study was conducted from 1985–1987 on the Lucy Islands (54°18'N; 130°37'W), an archipelago of small, low-lying, heavily forested islands located in Chatham Sound, 18 km west of Prince Rupert, British Columbia (see Fig. 1). Approximately 21,500 pairs of Rhinoceros Auklets breed on the islands, spread over most of the larger forested islands.

We studied growth on the Lucy Islands in 1983–1987, and at two other Rhinoceros Auklet colonies in 1984–1986. Pine Island (50°58'N; 127°41'W) is heavily forested and low-lying, has an estimated 67,000 breeding pairs and lies 10 km northeast of Vancouver Island. Triangle Island (50°52'N; 129°05'W) is an exposed, treeless, steep-sloped island 40 km northwest of Vancouver Island (Fig. 1). It is British Columbia's largest seabird colony and contains about 22,000 breeding pairs of Rhinoceros Auklet among more than half a million pairs of other seabird species. The three study colonies all lie in or immediately adjacent to the transitional zone between two major northeast Pacific production domains—the Coastal Downwelling Domain and the Coastal Upwelling Domain (Fig.

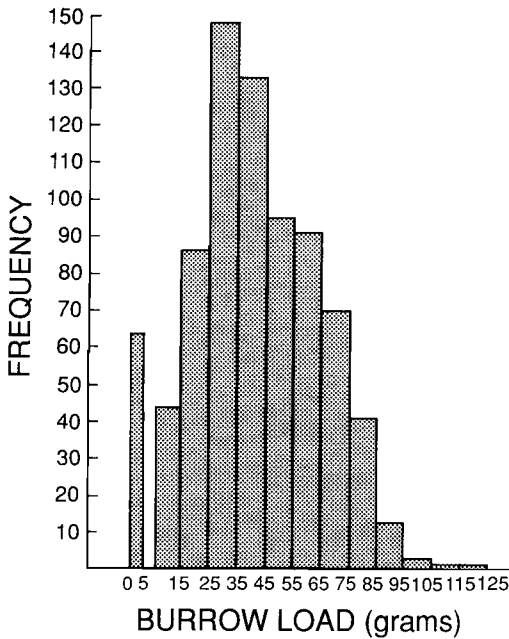


Fig. 2. Histogram of all 790 burrow loads collected in 1985–1987. The burrow loads are grouped into blocks of 10 g each; the numbers along the axis (except zero) represent the midpoint of the group. Zero represents burrow loads ranging from 0 to 5 g.

1). These are generated by large-scale wind and ocean patterns, and shifts in these patterns can cause the transition zone to be dominated by either the Downwelling or Upwelling domain (Ware and McFarlane 1989).

**Provisioning study.**—In each year 28 to 45 chicks were located in burrows on the Lucy Islands, and the amount of fish provided by their parents was measured. We fit the chicks with nylon hoods. Holes cut at the level of the nares permitted easy breathing, and a drawstring prevented chicks from removing the hoods (Hatch 1984). A burrow load ranged from no fish to three bill loads of fish. In 1985 some of the hooded chicks apparently wandered from their burrows and were lost. In 1986 and 1987, hooded chicks were tethered in the nest chamber by 15 cm of nylon mason cord attached to a bird band on the leg, and secured to a peg. This prevented wandering, and appeared to have no adverse effects on chicks, or on adult provisioning behavior. Hooding had no significant negative impact on the growth of auklet chicks relative to the growth of unhooded control chicks (Bertram 1988).

Experimental chicks were hooded on a rotating basis every fifth night from the onset to the termination of the experiment, or until they left the nest. Chicks were hooded in the evening between 1700 and 2200. The following morning each nestling was unhooded, and the uningested fish collected by systematically checking all tunnels of its burrow, through previously formed access holes. Following washing and measurement of the fish, chicks were fed their intended meal. We used mass-length regressions on samples collected in 1985 to calculate the total weight of fish in the load. For each year a *provisioning curve* was established by using a second degree polynomial equation to describe the relationship between burrow load and chick age. We determined chick age from a wing length–age regression established in 1985 from a sample of chicks whose hatching dates were known.

To estimate the size of bill loads, we captured adults on the colony as they returned at night with fish for their young. Sampling was never conducted in areas where experiments were underway, and repeat samples from the same area were separated by about 1 week to reduce disturbance to the birds.

**Growth study.**—The main growth study was carried out on the Lucy Islands in 1985–1987. We used regressions of nestling mass on age during the period between 10 and 40 days of age and the slope of the fitted relation as an estimate of the growth rate for each nestling. We call these growth measurements *sequential*. In 1987 the nestlings used in this study also participated in the hooding experiment (see above).

We constructed composite growth curves (Ricklefs and White 1975), on Lucy, Pine, and Triangle islands in 1984–1986, and in 1983 and 1987 on the Lucy Islands. To establish a composite growth curve, we measured a sample of chicks encompassing a wide range of developmental stages in early July on each island, and again 10 days later. We estimated the growth rate for chicks on each island in each year from the slope of a linear regression fitted to the full data set. The visits to the islands were carried out by the Canadian Wildlife Service and are reported in full by Bertram and Kaiser (1988).

## RESULTS

**Provisioning.**—Burrow loads ranged from 0 to 116 g, and the modal load was 30–35 g (Fig. 2). The mode corresponds with the mean ( $\pm$ SD) bill load measured on the Lucy Islands in 1985–1987 (1985:  $31.8 \pm 10.6$ ,  $n = 74$ ; 1986:  $34.1 \pm 10.6$ ,  $n = 212$ ; 1987:  $33.5 \pm 8.5$ ,  $n = 131$ ; overall:  $33.5 \pm 9.7$ ,  $n = 417$ ), which indicates that the majority of burrow loads are composed of a single bill load. The largest bill load we collected was only 55 g. The large burrow loads were likely composed of two or perhaps three separate bill loads. The loads were, by mass, >85%

Pacific sand lance, and there was no seasonal pattern in the appearance of other prey species (unpubl. data).

There were considerable differences between years in the pattern of burrow load deliveries as chicks aged. In 1985 burrow loads increased with chick age and peaked at around 30 days of age, then they declined steadily (Fig. 3a). The estimates for the two youngest age groups in 1985 are based on small samples; more importantly, they are underestimates. These were the first burrow loads we collected and, due to our inexperience, we probably missed finding parts of some burrow loads in the often intricate burrow systems. (We later found some of them in side branches.) These errors occurred only in these first two samples and the steepness of the increase in burrow load observed in 1985 is exaggerated, though we have no way of estimating by how much. In 1986 the burrow loads delivered to young chicks remained roughly constant until chicks were about 45 days old, after which they declined (Fig. 3b). In 1987 there was no decline in burrow-load size as chicks approached nest departure (Fig. 3c). The decline in burrow loads near the end of the season in 1985 and 1986 is valid according to the significant negative quadratic parameter of the polynomial equations (Table 1). The Chi-square coefficients differ significantly between years (1985-1986:  $t = 51.3$ ,  $df = 496$ ,  $P < 0.001$ ; 1986-1987:  $t = 30.8$ ,  $df = 501$ ,  $P < 0.001$ ). The shape of the provisioning curve could not be accounted for by changes in bill-load size because there was no consistent seasonal change in bill-load size (Bertram 1988), as reported by other workers (Leschner 1976, Wilson 1977, Hatch 1984).

The decline in provisioning in 1985 and 1986 might, as many investigators have suggested (e.g. Burger 1980), be due to a seasonal decline in the food available around the colony. To test this, we compared the provisioning of early- and late-hatched chicks, reasoning that if a seasonal decline were responsible, late-hatched chicks would be fed less than early-hatched chicks. Chicks were placed into groups hatched

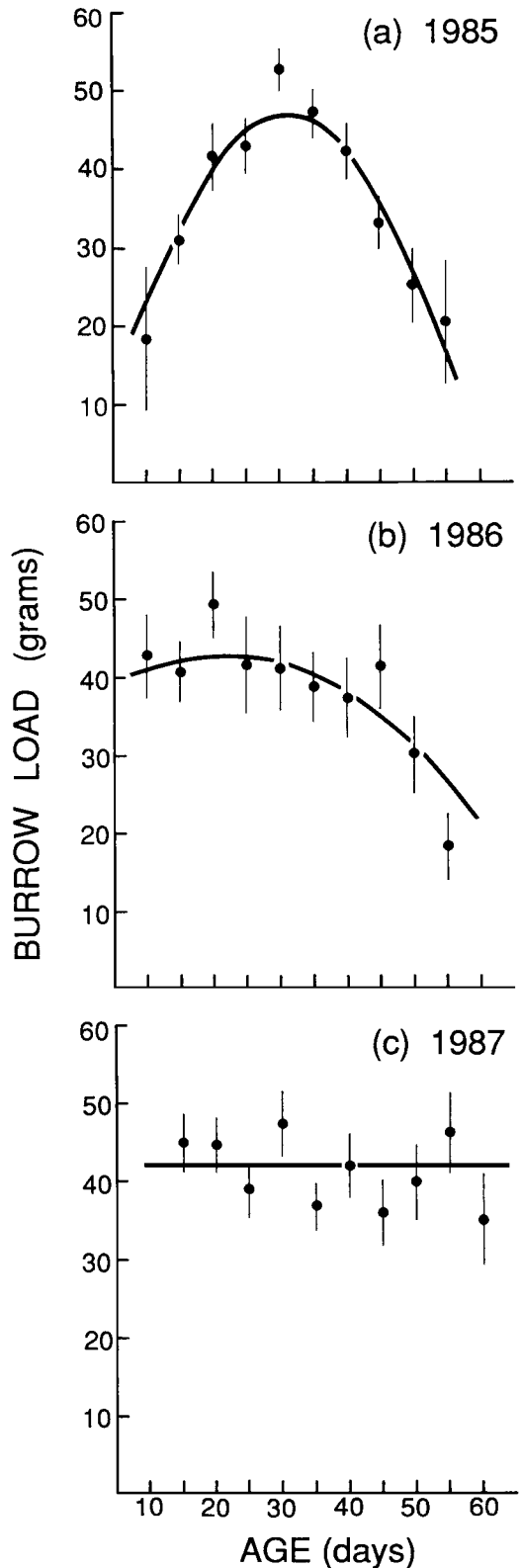


Fig. 3. Burrow loads delivered to hooded Rhinoceros Auklet chicks in relation to their age in 1985 (a), 1986 (b), and 1987 (c). For clarity group means ( $\pm$ SD) are shown, but the regression line shown is fitted to all points in each year.

TABLE 1. Coefficients of the regression equations fitted to the relationship of burrow load delivered and chick age (provisioning curves) in different years.

Year	Parameters			n
	Intercept ( $\pm$ SD)	Age (x) $\pm$ SD	Age <sup>2</sup> (x <sup>2</sup> ) $\pm$ SD	
1985	-8.2 $\pm$ 9.9	3.69 $\pm$ 0.64 <sup>a</sup>	-0.061 $\pm$ 0.009 <sup>a</sup>	287
1986	34.0 $\pm$ 9.6 <sup>a</sup>	0.87 $\pm$ 0.64	-0.019 $\pm$ 0.009 <sup>a</sup>	209
1987	51.5 $\pm$ 9.6 <sup>a</sup>	-0.49 $\pm$ 0.59	0.005 $\pm$ 0.008	294
1985-1987	30.9 $\pm$ 5.6 <sup>a</sup>	0.97 $\pm$ 0.36 <sup>a</sup>	-0.018 $\pm$ 0.005 <sup>a</sup>	790

<sup>a</sup> Significantly different from zero with  $\alpha = 0.05$  for one-tailed tests.

within 5 days of each other. To compare the mean burrow load fed to the different birth-date groups as they aged, we used Friedman's method for randomized blocks (outlined by Sokal and Rohlf 1981: 445). The procedure involved ranking the burrow loads across birth-date groups for each age category considered, essentially comparing the burrow loads fed to early and late chicks while holding age constant.

The rankings of burrow loads indicated that there was no significant difference in the weight of burrow loads fed to chicks of the same age "early" and "late" in the season in any of the three years (Table 2). Unfortunately the statistical power of these comparisons is low, and it is unlikely that a difference of the magnitude we estimate would have been detectable with our sample (Bertram 1988).

*Growth.*—We also compared the growth rate of early- and late-hatched chicks. Data are available from 1986 and 1987, and in neither year was late chicks' growth significantly slower (Table 3). Thus neither provisioning nor growth measurements supported the idea that late-hatched chicks were fed less.

We found significant differences among years in growth rate. In the years 1984-1986 (for which we have composite growth estimates on all colonies), growth was fastest in 1985 on all the colonies, slowest in 1986, and intermediate in 1984 (Table 4). For the Lucy Islands we found a rise in growth rates from 1983 to 1985, and a decrease from 1985 to 1987. The sequential growth measurements made on the Lucy Islands were similar. Though the estimates made by this method are lower than those given by the composite method, their ranking is the same.

TABLE 2. Burrow loads (g) delivered to chicks hatched on different dates in 1985-1987.

Year/hatching date	Chick age (days)									
	10	15	20	25	30	35	40	45	50	55
1985 <sup>a</sup>										
4-9 July	25.2	35.7	68.8	44.4	33.7	40.2	61.6	—	—	—
29 June-3 July	0.0	30.4	46.3	51.1	66.2	55.4	28.9	39.9	14.5	—
23-28 June	21.3	28.9	37.6	37.4	54.3	42.3	33.3	37.1	25.6	—
17-22 June	—	37.1	40.6	49.3	47.2	44.4	44.7	26.3	30.0	22.9
11-16 June	—	—	18.1	31.8	53.4	53.4	60.3	32.6	19.8	14.0
1986 <sup>b</sup>										
16-21 July	38.2	32.8	29.7	14.2	18.5	—	—	—	—	—
10-15 July	46.6	37.8	17.0	27.6	19.5	—	—	—	—	—
4-9 July	40.8	61.2	61.2	29.5	33.5	42.9	34.1	—	—	—
29 June-3 July	—	42.8	68.6	25.2	17.4	49.7	73.9	—	—	—
23-28 June	42.9	40.2	51.0	38.4	48.9	46.9	34.7	—	—	—
1987 <sup>c</sup>										
23-28 June	—	40.7	52.4	35.1	40.1	37.7	43.4	32.7	22.3	—
11-16 June	—	48.3	37.7	42.4	54.2	36.1	40.8	39.4	56.2	—

<sup>a</sup> Friedman's analysis (see text) performed on chick ages 20-40 days:  $n = 195$ ;  $\chi^2 = 3.04$ ;  $df = 4$ ,  $P > 0.05$ ; NS.

<sup>b</sup> Analysis performed on chick ages 15-30 days:  $n = 103$ ;  $\chi^2 = 8.6$ ;  $df = 4$ ,  $P > 0.05$ ; NS.

<sup>c</sup> All data in analysis  $n = 276$ ;  $\chi^2 = 0.5$ ;  $df = 1$ ,  $P > 0.05$ ; NS.

TABLE 3. Mean ( $\pm$ SD) growth rates (g/day) based on sequential measurements of chicks hatched early and late on the Lucy Islands in 1986 and 1987. There is no significant tendency for later-hatched chicks to grow more slowly.

Year/hatching date	Growth rate	<i>n</i>	<i>F</i>	<i>P</i>
1986				
23-28 June	5.79 $\pm$ 1.39	17	2.18	0.139
29 June-3 July	3.76 $\pm$ 1.24	2		
4-9 July	4.55 $\pm$ 2.41	4		
1987				
11-16 June	5.79 $\pm$ 1.81	16	0.96	0.346
23-28 June	5.50 $\pm$ 1.19	17		

Growth rates were highest in 1985 and lowest in 1987 (Table 5). We found consistent differences among the three colonies (Table 4). Growth rate was always highest on the Lucy Islands, and lowest on Pine Island. Moreover, Pine and Triangle islands were always more similar to each other than to Lucy, commonly 67-80% of the growth rate on the Lucy Islands.

#### DISCUSSION

Provisioning and the growth of Rhinoceros Auklet chicks were significantly different among the years of our study (Fig. 3, Table 1). Chick growth was fastest in 1985 (when provisioning was terminated most rapidly) and slowest in 1987 (when provisioning was most prolonged and did not decline). Rhinoceros Auklet chick growth at all three colonies rose and fell synchronously during the study (Table 4). We suggest that an oceanic phenomenon influences the entire region and somehow affects the birds. A mechanism to produce such a large-scale influence was postulated (Ware and McFarlane 1989). Several independent lines of evidence also suggest that ocean production in the region increased following a low in 1983, peaked in 1985, and fell again in 1986 and 1987.

TABLE 5. Mean ( $\pm$ SD) nestling growth rates (g/day), based on sequential measurements, in 1985-1987 on the Lucy Islands. Sample sizes are in parentheses.

Year	Growth rate <sup>a</sup>
1985	7.10 $\pm$ 2.58 (14)
1986	5.40 $\pm$ 1.66 (23)
1987 <sup>b</sup>	5.25 $\pm$ 1.52 (33)

<sup>a</sup> *F* = 5.68; *df* = 2, 67; *P* = 0.004. A Student-Newman-Keuls multiple-range test indicates that 1985 differs from 1986 and 1987, and that 1986 and 1987 do not differ from each other.

<sup>b</sup> Chicks also participated in the hooding experiment.

Following the 1982/1983 El Niño-Southern Oscillation (ENSO) event, a warm-water mass moved northward along the western North American coastline (see Mysak et al. 1982). In the upwelling and transitional regions (Fig. 1), this warm-water mass apparently suppressed upwelling and hence productivity. In upwelling systems, cold saline surface waters are most productive (e.g. Barber and Chavez 1983). We therefore assume that sea surface temperature and salinity records can, taken together, provide a crude index of ocean production. Ocean temperature (Fig. 4a) and salinity (Fig. 4b) at northern light stations along the British Columbia coast indicate that, after the major 1982/1983 ENSO event, production dropped, then rose, and peaked in 1985; it has since declined again. In addition, records of zooplankton production (1985-1987; Thomson and Ware 1988), fish fauna and marine salmonid survival (K. Hyatt pers. comm.) and herring recruitment (Haist and Schweigert 1989) support this interpretation of fluctuations in ocean production. Although it is not clear that the ENSO event was itself entirely responsible for the observed pattern, the available evidence is consistent with a 1985 peak in production. The postulated mechanism fits with the pattern in growth measured at the three colonies and also explains why they all showed the same pattern.

The 1982/1983 ENSO (the strongest of such

TABLE 4. Growth rates (g/day) of Rhinoceros Auklet chicks on three British Columbia colonies (1983-1987), estimated from the composite growth curve. The standard error for the slope estimates ranges from 0.04 to 0.1. The sample size is given in parentheses.

Colony	1983	1984	1985	1986	1987
Lucy Islands	7.2 (42)	8.9 (38)	10.8 (30)	8.0 (21)	5.4 (33)
Pine Island		6.2 (68)	7.2 (53)	5.9 (59)	
Triangle Island		6.7 (53)	7.4 (49)	6.4 (40)	

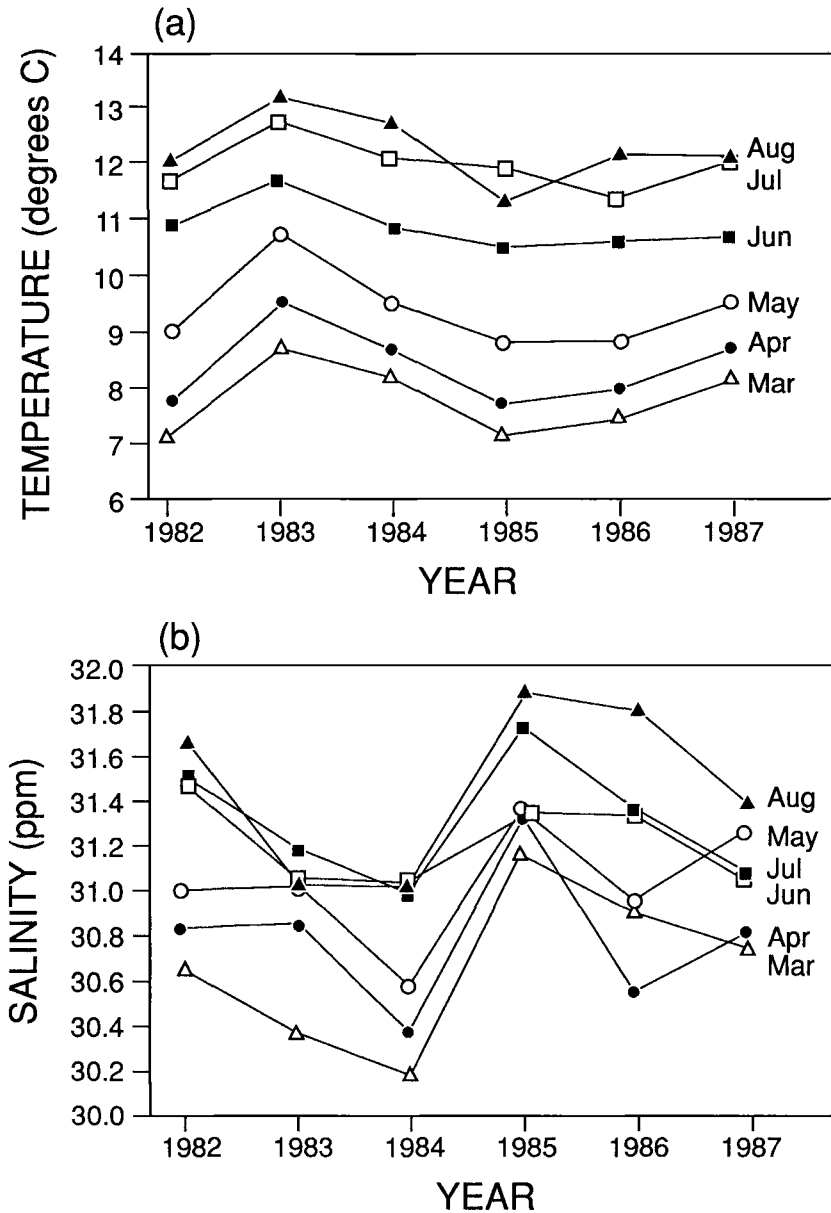


Fig. 4. Mean monthly sea-surface temperatures (a) and salinities (b) from 1982-1987 taken from northern light stations in British Columbia (Mar. Environ. Data Syst., Canada Dep. Fish. Oceans, unpubl.). The months chosen encompass the developmental period of the larvae and juvenile sand lance that predominate the nestling diet. Salinity measurements were taken from Bonilla, Kains, Langara and Pine Islands. Temperature was taken from these islands as well as St. James and Egg Island.

events on record (Mysak 1986)) has been considered a factor in seabird mortality and reproductive failure in Peru (Duffy 1983, Hays 1986), the central Pacific (Schreiber and Schreiber 1984), Oregon (Hodder and Graybill 1985, Bayer 1986) and as far north as Alaska (Hatch 1987)

(see Ainley et al. 1988 for a comprehensive review). In most cases, changes in prey populations (primarily fish) were considered basic to the problems. There has been some debate as to whether shifts in the distribution of fish prey populations render them unavailable to birds

(e.g. Duffy 1983) or whether fish abundance declines as a result of the decrease in primary productivity (e.g. Barber and Chavez 1983). In Peru the evidence suggests that the 1982/1983 ENSO disrupted the normal food web, and it decreased growth and reproductive success for most species of higher trophic levels (Barber and Chavez 1983). The consequences of such oceanographic changes depend on location and prey species under consideration. Regardless, in any attempt to link events on seabird colonies to oceanographic fluctuations, the question concerning prey abundance or availability will arise (e.g. Briggs et al. 1983, Springer et al. 1984, Baird 1990). One thing that has become clear from such studies is that different seabird species will respond to changes in oceanographic/feeding conditions in different ways (e.g. Ainley et al. 1988, Hatch and Hatch 1990).

In our study, ocean temperature was lowest and salinity was highest in 1985 (Fig. 4: a, b) suggesting a peak in productivity in that year. Moreover, in 1985, year-class-1 sandlance (see Vermeer and Westrheim 1984) dominated the bill loads in all three seabird colonies, something which happened in no other year (Bertram and Kaiser 1988). We suggest that a high degree of ocean productivity lead to a strong year-class for sandlance along the entire northern British Columbia coast in 1985. Although a discussion of recruitment variation in sandlance is beyond the scope of this paper, for a number of marine fishes in the Northeast Pacific Ocean, recruitment success is strongly influenced by environmental conditions (Hollowed et al. 1987). In British Columbia there is no commercial fishery for sandlance, which may allow for more direct linkage among ocean production, prey populations, and events on seabird colonies than in systems where seabird prey are harvested commercially. (For a discussion, see Crawford and Shelton 1978, Furness and Cooper 1982, MacCall 1984 and Montevecchi et al. 1988.)

Our measures of provisioning on the Lucy Islands revealed patterns that changed in step with indices of ocean productivity on the British Columbia coast. Parental provisioning reached approximately the same peak level in each of the three years, but it declined most rapidly in the year of higher productivity and not at all in the year of lowest productivity. In many semiprecocial alcid species the rate of parental provisioning progressively declines dur-

ing the later part of the nestling period (Atlantic Puffin [Harris and Hislop 1978, Ashcroft 1979, Hudson 1979], Pigeon Guillemot, *Cephus columba* Pallas [Emms 1987], and Black Guillemot, *C. grylle* L. [Cairns 1987a]). In Rhinoceros Auklets the decline seems to result from fewer parental visits, rather than from a reduction of the load delivered on each visit. We conclude this because bill loads show no systematic decline in mass in the latter part of the nestling period. The decline in burrow loads must occur because parents make fewer visits toward the end.

One hypothesis to explain the decrease in feeding trips is that there is a seasonal decline in abundance of food in the region surrounding the colony (e.g. Burger 1980). This "seasonal deterioration" hypothesis is rejected by our study on two grounds. We found no evidence that later-hatched chicks grew significantly slower than early chicks, as would be expected if there was a seasonal decline in the availability of food. Nor did the analysis of the size of burrow loads delivered to chicks hatching on different dates (Table 2) indicate any consistent seasonal decline. Although the statistical power of the test was low, and we cannot entirely rule out the possibility of a seasonal effect, it seems unlikely to be large compared with the effect of chick age on parental provisioning. Rhinoceros Auklets in the Gulf of Alaska are provisioned by adults according to the age of the chick but not according to the time of the season (Hatch 1984). Evans (1981) reported a similar result in Dovekies (*Alle alle* L.) in Greenland. The inability to detect a seasonal effect on the size of burrow loads suggests that the seasonal deterioration hypothesis is insufficient to account for the observed decline in feeding rate to chicks in the late stages of development. Moreover, growth in 1985 was "good" at all three colonies studied. The seasonal deterioration hypothesis would predict the opposite because provisioning declined most rapidly in that year.

A second hypothesis to explain the decline in provisioning holds that the decline reflects the decreasing energy demands of older nestlings. In the Pigeon Guillemot (Koelink 1972) and the Dark-rumped Petrel (*Pterodroma phaeopygia sandwichensis* Ridgway; Simons and Whitow 1984), the energy budget peaks in the middle of the development period and then falls toward fledging. Provisioning curves should be similar from year to year if parent Rhinoceros



Auklets provision chicks based on the chick's energetic needs. The fact that the provisioning curves are so different from year to year suggests that this hypothesis is insufficient to account for the variable decline in feeding rates as chicks approach fledging.

A corollary of the chick-energetics hypothesis is that chick fledging weights should be similar between years. Although we have no supporting data from our study, mean fledging weights on Triangle Island ranged from 51 to 69% of adult body weight in 1975–1978 (Vermeer and Cullen 1979). The fact that fledging weights were more variable between years than within years (Vermeer and Cullen 1979) also argues against the chick-energetics hypothesis.

We suggest that parental provisioning was affected by interannual changes in ocean production, but the manner in which these large-scale changes were manifested in the provisioning of nestlings is not obvious. A possible explanation is that parents vary provisioning from year to year according to the postfledging survival prospects of their offspring, which in turn are affected by annual changes in ocean conditions. Although we presently have insufficient data to test this idea, it appears to warrant further attention. For parental Rhinoceros Auklets the colony is believed to be a dangerous environment. For example, Bald Eagles (*Haliaeetus leucocephalus* L.) are known to congregate on colonies and prey on auklets as they arrive or depart (DeGrange and Nelson 1982, Kaiser 1989). Consequently, we propose that when food availability is high and the survival of chicks at sea is likely to be high (as in 1985), selection favors parents that fledge young early, which increases their own survival prospects. Clark and Ydenberg (1990; see also Ydenberg 1989) showed theoretically that predation risk at seabird colonies selects for "reluctant" parents, who cease provisioning when possible (see Norton-Griffiths 1969, Hauser and Fairbanks 1988).

It has been advocated repeatedly that seabird chick diets and growth rates may act as indicators of marine resources (e.g. Cairns 1987b). However, despite the fact that parent seabirds are capable of working harder than normally (reviewed by Ydenberg and Bertram 1989), we know very little about how parental provisioning effort should vary with chick age in response to a range of ocean feeding conditions. Although our study implicates large-scale fluctuations in ocean productivity as the dominant

influence upon provisioning patterns of British Columbia Rhinoceros Auklets, the manner in which parents should respond to such environmental variation remains open for investigation.

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