Diving depths, diet, and underwater foraging of Rhinoceros Auklets in British Columbia

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Rhinoceros Auklets (*Cerorhinca monocerata*) were studied at Triangle Island, Cleland Island, and Seabird Rocks, British Columbia, in 1986–1989. Epipelagic schooling fish were consistently the most common prey delivered to auklet chicks at all three localities. Pacific sand lance (*Ammodytes hexapterus*), Pacific herring (*Clupea harengus*), juvenile salmon (*Onchorhyncus* spp.), Pacific saury (*Cololabis saura*), and juvenile rockfish (*Sebastes* spp.) were important prey. Bite marks on the fish showed that 73% were attacked from below. The mean deepest depth recorded for 16 auklets was 30 m (range 12–60 m). Eleven time-at-depth records showed that the auklets were epipelagic foragers: 90% of the mean underwater time was spent in the upper 10 m, although most birds had a few deeper dives of 20–60 m. Shipboard transects showed that Rhinoceros Auklets usually foraged in water considerably deeper than 15 m. A model of diving efficiency indicated that a relatively large proportion (>40%) of the average dive cycle was spent foraging rather than travelling or resting, and prolonged dives invoking anaerobic glycolysis were avoided. We discuss the implications of diving limitations on foraging behaviour and the use of Rhinoceros Auklets as indicators of prey availability.

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Les Macareux rhinocéros (*Cerorhinca monocerata*) ont été étudiés dans les îles Triangle et Cleland et à Seabird Rocks, en Colombie-Britannique, de 1986 à 1989. Les bancs de poissons épipélagiques sont toujours la source la plus abondante de proies apportées aux oisillons aux trois endroits. Le Lançon gourdeau (*Ammodytes hexapterus*), le Hareng du Pacifique (*Clupea harengus*), les saumons (*Onchorhyncus* spp.) juvéniles, le Balaou japonais (*Cololabis saura*) et les jeunes sébastes (*Sebastes* spp.) sont des proies importantes. Les traces de morsure sur les poissons indiquent qu'environ 73% sont attaqués par dessous. La moyenne des profondeurs maximales atteintes par 16 oiseaux a été évaluée à 30 m (étendue 12–60 m). Onze séries de données sur le temps passé à une profondeur particulière indiquent que les macareux sont épipélagiques; 90% de la durée moyenne des plongées se passait dans les 10 m supérieurs de la colonne d'eau, bien que la plupart des oiseaux aient procédé à quelques plongées plus profondes de 20–60 m. Des transects suivis à bord d'un bateau ont démontré que les macareux cherchent habituellement leur nourriture à des profondeurs beaucoup plus grandes que 15 m. Un modèle illustrant l'efficacité des plongées indique qu'une proportion relativement importante (>40%) du cycle moyen de plongée est mise à profit pour chercher de la nourriture plutôt que pour se déplacer ou se reposer, et que les plongées prolongées qui font appel à la glycolyse anaérobique sont évitées. Nous étudions les conséquences des limites de la capacité de plongée sur le comportement de recherche de nourriture et examinons la possibilité d'utiliser les Macareux rhinocéros comme indicateurs de la disponibilité des proies.

[Traduit par la rédaction]

Introduction

Pelagic seabirds are among the most frequently studied marine organisms, but much of their feeding ecology remains poorly known because they often feed far offshore. Diving seabirds present special challenges because their activities underwater are difficult to observe and quantify. In the past two decades the development of devices to measure swimming speed (Wilson and Bain 1984), diving depth (Kooyman et al. 1971, 1982; Wilson et al. 1989; Croll et al. 1992), activity budgets (Cairns et al. 1987), and position at sea (Wilson et al. 1991*b*) have greatly facilitated research on diving birds. Theoretical and laboratory studies have focussed on physiological limitations and optimal foraging strategies in diving birds (e.g., Kramer 1988; Kooyman 1989; Ydenberg and Clark 1989; Burger 1991), but the ecological implications have seldom been rigorously examined in field studies. Data on underwater foraging behaviour are particularly sparse for the family Alcidae, the dominant diving seabirds of the temperate northern hemisphere.

We report on the diving and underwater foraging behaviour of Rhinoceros Auklets (*Cerorhinca monocerata*) breeding at three colonies in British Columbia. This alcid is abundant and widespread in the temperate North Pacific. Several studies have analysed the prey delivered to chicks in the nest burrows: in Japan (Watanuki 1987), Alaska (Hatch 1984), British Columbia (Vermeer 1979, 1980; Vermeer and Westrheim 1984; Vermeer and Devito 1986; Bertram et al. 1991) and

TABLE 1. Percentage of total mass of prey species delivered to chicks of Rhinoceros Auklets at three colonies in British Columbia

Prey species	Common name	Triangle Island, 1986	Seabird Rocks, 1986	Seabird Rocks, 1987	Seabird Rocks, 1988	Cleland Island, 1988
Loligo opalescens	Squid	1.0	1.6	—	—	—
Clupea harengus	Herring	—	15.0	12.5	33.2	0.6
Engraulis mordax	Anchovy	—	5.1	—	—	—
Onchorhynchus tsawytscha	Chinook	—	—	12.3	—	—
Onchorhynchus keta	Chum	1.2	—	3.3	11.6	—
Onchorhynchus kisutch	Coho	—	—	2.6	—	—
Onchorhynchus sp.	Salmon sp.	6.1	17.2	—	—	—
Allosmerus elongatus	Whitebait smelt	—	0.6	0.8	4.3	—
Hypomesus pretiosus	Surf smelt	—	22.2	21.9	41.4	—
Cololabis saura	Saury	28.7	—	—	—	—
Trichodon trichodon	Sandfish	—	8.6	0.6	—	—
Ammodytes hexapterus	Sand lance	42.0	29.1	45.9	9.5	95.8
Sebastes sp.	Rockfish	17.0	0.2	—	—	3.6
Hexagrammos decagrammus	Greenling	4.0	0.5	—	—	—
Flounder sp.	Flounder	0.1	—	—	—	—

NOTE: See Appendix for additional data on numbers and sizes of prey.

Washington (Richardson 1961; Wilson and Manuwal 1986). The diet of adults is less well known (Vermeer et al. 1987). Relatively little is known about their foraging depths, dive times, manner of capturing prey, or the physiological limitations affecting their diving strategies. We address these topics using time-at-depth recorders, maximum depth gauges, detailed examination of prey items, and field observations.

The relative ease with which chick meals and chick growth rates can be measured has led to suggestions that Rhinoceros Auklets (Vermeer and Westrheim 1984; Bertram 1988; Bertram et al. 1991) and closely related puffins (Hatch and Sanger 1992) could be used to monitor the availability and population trends of selected fish species, and thus the effects of oceanic processes. Such monitoring studies would be most effective if the at-sea behaviour, depth limitations, and distribution of the birds could be well understood. Our study contributes to such understanding. We also sampled chick meals at three colonies to help understand the geographical and temporal variations in prey selection.

Methods

We studied Rhinoceros Auklets during the chick-rearing periods at three colonies off Vancouver Island, British Columbia: off the northwest tip of Vancouver Island at Triangle Island (50°52′N, 129°05′W; 12–23 July 1986), off Barkley Sound at Seabird Rocks (48°45′N, 125°09′W; 6–20 August 1986; 22 July – 17 August 1987; 26 July – 4 August 1988; 24–25 June 1989); and off Clayoquot Sound at Cleland Island (49°10′N, 126°05′W; 7–9 July 1988). The estimated breeding populations of Rhinoceros Auklets at these islands were 41 680, 130, and 990 pairs, respectively (Rodway 1991).

Adult auklets were trapped in mist nets or coarse-mesh baffle nets as they returned after dusk to feed their chicks. This was done to obtain prey samples (the adult auklets carry intact prey in their beaks) and to attach and recover depth gauges. A few adults were also caught by hand or with simple trap-doors set into the burrows. Birds were identified with leg bands. Prey items were collected in polythene bags. On the following morning they were weighed with a Pesola spring balance to the nearest 0.2 g and the fork lengths of the fish were measured to the nearest 1 mm. Where possible, discrete meals were kept separate, but in many cases where several adults were caught simultaneously, their meals became mixed together and had to be omitted from analyses requiring discrete meals. The few prey collected in 1989 at Seabird Rocks were insufficient for analysis of meals.

The bite marks inflicted by the auklets were clearly visible on many fish. Fish being transported in the beak were almost invariably held near the gills or just posterior to the head. In many instances we found a bite mark toward the rear of the fish that was inflicted with exceptional force. We interpreted this to be the initial bite inflicted as the bird caught the fish, and we recorded its position on a sample of fish.

Two types of depth gauge were deployed. Maximum depth gauges (MDGs) consisted of short (60–100 mm) lengths of flexible plastic tubing (Tygon brand; internal diameter 1.6 mm) lined with a light dusting of soluble indicator (icing sugar) and sealed at one end. These gauges recorded the single deepest depth attained by each bird. The operation, accuracy and possible errors of these gauges have been reviewed by Burger and Wilson (1988). Gauges that showed buildup of internal moisture droplets were discarded.

Time-at-depth recorders (TDRs) were constructed from 3 cm^3 disposable syringes following Wilson et al. (1989). Photographic film (Kodak Pan-X developed in Microdol) was used to record the depth-dependant position of a light-emitting diode mounted on the bung of the syringe (see Wilson et al. 1989 for details). The time at each depth was estimated from the optical density of the image left by the diode on the film, measured with a Schoeffel SD3000 spectrodensitometer with the width slit set at 0.3 mm. Time and depth calibrations were made by lowering each gauge for predetermined times to prescribed depths in seawater. The optical density was converted into a time estimate with reference to timed calibration exposures of film, and the error resulting from light spreading was reduced using the deconvolution procedure outlined by Wilson et al. (1989). These TDRs did not record time spent in the upper 2–5 m, because some initial pressure was required to move the bung. Versions of this TDR have been used in other avian studies (Burger and Powell 1990; Wanless et al. 1991; Wilson et al. 1991*a*, 1991*c*) and gave very similar results to another electronic TDR (Croll et al. 1992).

Our MDGs weighed <1 g, which was $<0.2\%$ of the mean adult body mass (520 g; Vermeer and Cullen 1979), and had a cross-sectional area (13 mm^2) about 0.2% of the cross-sectional area of the adult bird in mid-body (6793 mm^2; mean of five dead adults). Corresponding values for the TDR were 6 g (1.2% of adult mass) and 153 mm^2 (2.3% of adult cross-sectional area). Gauges were attached using a strip of waterproof adhesive tape wrapped around a few dorsal feathers. The gauge and the tape formed a streamlined package, which was positioned just posterior to the thickest part of the body

TABLE 2. Mean mass and number of prey in meals delivered to chicks of Rhinoceros Auklets

Site and year	No. of meals	Meal mass (g)*			No. of prey**		
		Mean	SD	Range	Mean	SD	Range
Triangle Island, 1986	73	30.5	14.2	5.9–68.7	5.8	3.3	1–12
Seabird Rocks, 1986	10	31.0	21.0	7.8–76.2	2.7	10.8	1–6
Seabird Rocks, 1987	18	30.7	12.3	13.5–57.1	5.9	3.3	1–13
Seabird Rocks, 1988	21	31.5	14.1	8.5–65.0	3.9	2.9	1–10
Cleland Island, 1988	36	26.4	9.6	8.0–51.0	7.3	3.1	3–19
All samples pooled	158	29.8	13.5	5.9–76.2	5.7	3.3	1–19

*ANOVA: $F_{[4,153]} = 0.724$, $P > 0.1$.
**ANOVA: $F_{[4,153} = 6.534$, $P < 0.001$.

TABLE 3. Percentage of meals of Rhinoceros Auklets that contained a single prey type, or more than one species, and some common combinations of prey species

	Triangle Island, 1986	Seabird Rocks, 1986	Seabird Rocks, 1987	Seabird Rocks, 1988	Cleland Island, 1988	All data combined
No. of species per meal						
1	50	57	58	67	81	60
2	34	21	37	33	19	30
3	15	14	5	0	0	9
4	1	7	0	0	0	1
Common combinations						
Ammodytes – Sebastes	21	7	0	0	11	13
Hexagrammos – Sebastes	17	0	0	0	0	8
Ammodytes – Clupea	0	7	26	10	8	6
Cololabis – Sebastes	12	0	0	0	0	6
Ammodytes – Hexagrammos	11	0	0	0	0	5
Ammodytes – Onchorhynchus	4	14	11	0	0	5
Onchorhynchus – Sebastes	7	0	0	0	0	4
Ammodytes – Allosmerus	0	7	0	10	0	2
Total no. of meals examined	82	14	19	21	36	172

to further reduce drag as the bird moved through the water (Croll et al. 1991*b*). Gauges could be removed from recaptured birds without the loss of feathers, and those on birds not recaptured would fall off as the tape lost its adhesiveness or the bird moulted.

The distribution of Rhinoceros Auklets over sea of various depths was measured during transects undertaken by small vessels (4 – 10 m in length) at three locations. A single transect of 15.2 km was run off the Scott Islands, between Triangle Island and Jepther Point (Goletas Channel), on 23 July 1986, between 12:46 and 15:36, through an area where birds from the large Triangle Island and Pine Island colonies foraged. Five replicate weekly transects were run off Barkley Sound between 22 July and 19 August 1987, from 08:00 to 12:30, along an L-shaped route of 16.6 km, from Trevor Channel past Cape Beale to the open ocean and then south to Seabird Rocks. Fourteen weekly replicate transects of 9.5 km were run east of the Saanich Peninsula between Tsehum Harbour, Sidney, and Mandarte Island, between 15 May and 13 August, from 09:00 to 12:00. In each survey, Rhinoceros Auklets on the water were counted in 1-min intervals within a 300 m wide strip (150 m on either side of the vessel). The water depth was measured at regular intervals (every 1 min at the Scott Islands and Cape Beale, and every 2 min off Saanich) using an echosounder (Cape Beale and Saanich) or a navigation chart (Scott Islands).

Results

Composition and size of meals delivered to chicks

Fourteen species were identified in the 1137 prey items examined at the 3 sites (Table 1, Appendix). All were fish, except for six small squid (*Loligo opalescens*). Small schooling fish were consistently the most common prey, although species composition differed among the three sites: Pacific sauries (*Cololabis saura*) and rockfish (*Sebastes* spp.) were important only at Triangle Island; herring (*Clupea harengus*) and juvenile salmon (*Onchorhynchus* spp.) were important in all years at Seabird Rocks, but not elsewhere; the relatively large-bodied surf smelt (*Hypomesus pretiosus*) was seldom common, but was important at Seabird Rocks, especially in 1986. Sand lance (*Ammodytes hexapterus*) were important at all sites and in all years. They accounted for 42, 32, and 96% of the combined mass of prey from Triangle Island, Seabird Rocks (mean of 4 years), and Cleland Island, respectively. The prey items ranged in size from relatively large Pacific saury (mean mass 24.6 g) and surf smelt (mean 25.8 g) down to juvenile rockfish and greenling, some of which weighed < 1 g (see Appendix).

The average chick meal comprised 5.1 fish (range 1 – 19) and had a mass of 30.0 g (range 5.9 – 76.2 g). Comparisons among the five sampling periods showed no significant differences in the mean mass of chick meals, but the number of prey per meal did differ significantly (Table 2). Overall, meals comprised fewer prey at Seabird Rocks in 1986, although the mean mass per meal was high (Table 2). At Cleland Island, where meals were dominated by sand lance of relatively uniform size, we found a significant correlation between the num-

TABLE 4. Percentage of meals in which the stated prey species was found in mixed-species meals

Prey species	Common name	Triangle Island, 1986	Seabird Rocks, 1986	Seabird Rocks, 1987	Seabird Rocks, 1988	Cleland Island, 1988	All sites combined
Loligo opalescens	Squid	100 (3)	0 (1)	—	—	—	75 (4)
Clupea harengus	Herring	—	75 (4)	71 (7)	30 (10)	100 (3)	58 (24)
Engraulis mordax	Anchovy	—	100 (2)	—	—	—	100 (2)
Onchorhynchus spp.	Salmon spp.	88 (8)	100 (3)	75 (4)	33 (3)	—	78 (18)
Allosmerus elongatus	Whitebait smelt	—	100 (1)	100 (1)	100 (3)	—	100 (5)
Hypomesus pretiosus	Surf smelt	—	0 (3)	50 (4)	29 (7)	—	29 (14)
Cololabis saura	Saury	62 (21)	—	—	—	—	62 (21)
Trichodon trichodon	Sandfish	—	0 (1)	100 (1)	—	—	50 (2)
Ammodytes hexapterus	Sandlance	57 (37)	100 (4)	46 (11)	100 (5)	20 (35)	46 (92)
Sebastes sp.	Rockfish	72 (50)	100 (1)	—	—	80 (5)	73 (56)
Hexagrammos decagrammus	Greenling	100 (19)	100 (1)	—	—	—	100 (20)
Pleuronectidae (?)	Flounder	100 (1)	—	—	—	—	100 (1)

NOTE: Values are percentages followed by N in parentheses.

TABLE 5. Percentage of fish caught on the ventral surface (from below) by Rhinoceros Auklets

Prey species	Common name	Mean prey mass (g)	Caught from below (%)	N
Clupea harengus	Herring	4.5	92	26
Engraulis mordax	Anchovy	12.3	100	2
Onchorhynchus sp.	Salmon sp.	13.5	81	16
Allosmerus elongatus	Whitebait smelt	6.4	75	4
Hypomesus pretiosus	Surf smelt	26.6	100	10
Cololabis saura	Saury	24.6	100	3
Ammodytes hexapterus	Sandlance	4.4	68	170
Sebastes sp.	Rockfish	1.9	73	33
Hexagrammos decagrammus	Greenling	3.0	67	3
All species combined			73	267

ber of prey per meal and meal mass (Pearson $r^2 = 0.797$, $n = 10$, $P < 0.01$), but in all other sample periods there was no significant correlation ($P > 0.05$). In other words, meals consisting of a few large fish were similar in mass to those of many smaller fish.

Although 14 prey species were identified, 60% of the meals consisted of a single species, and only 1% contained more than 3 species (Table 3). This trend was consistent in all the sample periods, but the species that commonly occurred together in meals varied greatly among sites, and to a lesser extent among years at Seabird Rocks (Table 3). Salmon, whitebait smelt (*Allosmerus elongatus*), saury, rockfish, and greenling were found most often in mixed-species meals (Table 4).

Analysis of bite marks on prey fish

Inspection of 267 fish showed that 73% were caught from below (Table 5). The large surf smelt and sauries were invariably caught from below (Table 5), but analysis of sand lance and other fish showed no significant variation with size (Fig. 1; for sand lance, $\chi^2 = 6.11$, df $= 4$, $P > 0.05$; for all fish combined, $\chi^2 = 6.49$, df $= 5$, $P > 0.05$). Most of the capture marks were on the posterior portion of the fish, which was to be expected if the auklets pursued active prey (Fig. 2).

In a few cases, by measuring the width of the bite marks in the head region, we were able to determine the sequence in which a series of fish constituting a single meal were fitted into the adult auklet's gape. Of these, 93% (13 out of 14) of meals that contained one large fish (>20 g) together with several smaller fish (usually rockfish of about 1–3 g) had the larger fish closest to the gape. This suggests that the large fish was caught before the smaller ones, but we could not rule out the possibility that the fish were re-arranged in the beak after capture.

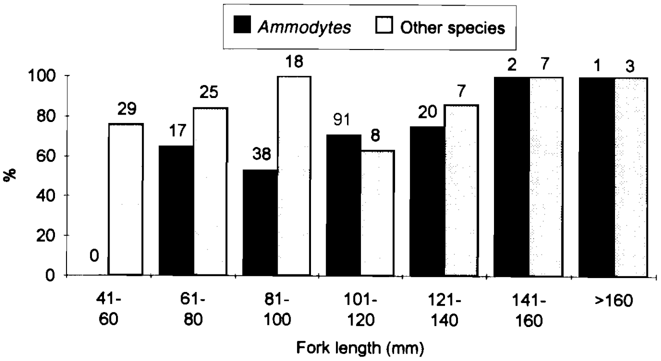

FIG. 1. Percentage of each size class of sand lance (*Ammodytes hexapterus*) and other fish that were captured from below by Rhinoceros Auklets, as indicated by bite marks on the fish. Numbers above columns indicate the number of fish sampled.

TABLE 6. Recovery rates of maximum depth gauges (MDGs) and time-at-depth recorders (TDRs) attached to Rhinoceros Auklets at three islands in British Columbia

Site and year	No. of recovery nights	MDGs		TDRs	
		No. attached	% recovered	No. attached	% recovered
Triangle Island, 1986	5	30	13.3	20	15.0
Seabird Rocks, 1986	4	0	—	13	38.5
Seabird Rocks, 1987	6	70	5.7	15	13.3
Seabird Rocks, 1988	3	6	16.7	11	18.2
Cleland Island, 1988	2	10	0.0	12	8.3
Overall	20	116	8.9	71	18.7

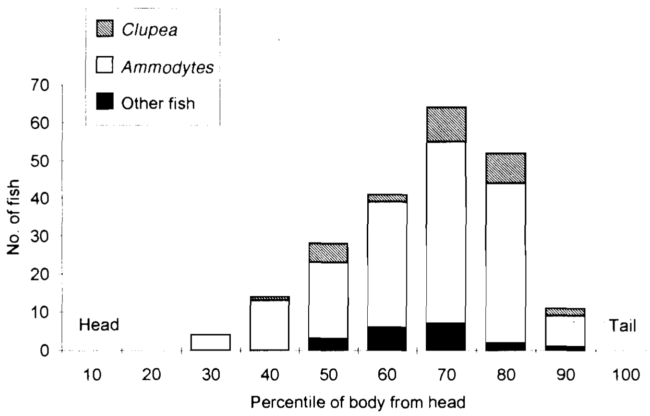

FIG. 2. Distribution of capture bite marks along the length of herring (*Clupea harengus*), sand lance (*Ammodytes hexapterus*), and other prey fish, beginning at the head (0%) and ending at the tail (100%). Most fish were first seized in the posterior half by Rhinoceros Auklets.

Rates of recovery of depth gauges

TDRs were fitted only on adults delivering food to chicks. On average, 19% of these devices were recovered (Table 6). MDGs were attached to several birds of indeterminate status, which probably included nonbreeding prospecting birds, and consequently their recovery rates were lower than for TDRs (Table 6). Variation in recovery rates among the sites and among years at Seabird Rocks was probably due to differences in recovery effort (the number of nights in which nets were set to recapture tagged birds, and the numbers of nets used), weather, and illumination (birds appeared to avoid nets on clear, moonlit nights). We minimized our activities at the colonies by restricting our netting to a few nights and never netted for more than two nights in succession. Two birds were weighed before and after the deployment of TDRs. One lost 23 g (4% of original 558 g mass) over 16 days, the other gained 5 g (1% of original 485 g) in two days.

Results from depth gauges

Maximum depths recorded by the MDGs and TDRs are shown in Table 7. The shallow reading of 4 m came from a bird recaptured 8 h after deployment, on the same night, and probably reflects bathing and not feeding activities. With this result excluded, maximum depths averaged 30 m (SD = 15 m, range 12–60 m, $n = 16$). Maximum depths from Triangle Island and Seabird Rocks did not differ significantly (Mann–Whitney test, $U_{[9,3]} = 28.5$, $P > 0.05$). TDRs and MDGs were deployed together on three birds. The results were identical in two cases and differed by 7% in the third (Table 7).

Leakage of light or water destroyed two TDR traces, but readable traces were obtained from 11 birds (Fig. 3). Most gauges were deployed for 1–3 days. Although they were capable of reaching 55–60 m in depth, on average the birds spent 90% of their time underwater in the upper 10 m, with progressively less time at greater depths (Figs. 3 and 4). In a few cases (e.g., samples 8623 and 8629T) the birds were clearly foraging for significant periods at depths of 10–40 m. A striking feature is that most birds made brief forays, perhaps one or two brief dives, into depths that were 10–30 m deeper than their preferred foraging depth (Fig. 3).

Chick meals were collected from five adults at the time the TDRs were recovered, giving some indication of the types of prey taken in the depths reported. The masses of these meals (28.0, 30.7, 32.5, 42.0, and 43.5 g) were all close to, or above, the average (30 g) recorded in this study (see also Wilson and Manuwal 1986; Vermeer 1980). Two auklets at Seabird Rocks in 1986 (samples 8609 and 8629) had caught juvenile salmon, sand lance, and whitebait smelt while foraging no deeper than 20 m, and predominantly in the upper 5 m. A bird that returned with a single large surf smelt (Seabird Rocks 8801) had gone comparatively deep (46 m) but foraged mainly in the upper 15 m. A mixed load of 5 herring and 2 sand lance came from a bird that dived to 34 m and foraged mainly in water <10 m (Seabird Rocks 8802). The single record from Cleland Island, where sand lance dominated in the meals, showed dives to 39 m with significant foraging at 10–15 m and at <5 m (sample 88CL).

Diving behaviour

It was difficult to monitor prolonged bouts of diving in Rhinoceros Auklets, even when watching birds foraging at close range. They swam large distances underwater, often in unpredictable directions, and often foraged in flocks of 2–5 birds making it impossible to distinguish individuals. The mean dive time (T_d) and inter-dive pause time (T_r) reported from adult auklets in 10 bouts (75 dives) were 45.0 and 10.8 s, respectively (Table 8). The longest dive was 69 s. The relationship between T_r and T_d for adults was almost linear and fitted the equation

$$[1] \quad T_r = 0.18\, T_d^{1.06} \; (r^2 = 0.15, \mathrm{df} = 68, P < 0.01)$$

A newly fledged juvenile had much shorter dives and longer pauses than the adults (Table 8).

TABLE 7. Maximum diving depths recorded for Rhinoceros Auklets using maximum depth gauges (MDGs) and time-at-depth recorders (TDRs)

Site	Date gauge recovered	No. of days deployed	Gauge type	Max. depth (m)	Notes[a]
Triangle Island	16 July 1986	1	MDG	21	
Triangle Island	17 July 1986	1	MDG	27	
Triangle Island	17 July 1986	1	MDG	19	
Triangle Island	17 July 1986	0.33	MDG	4	Bathing only?
Triangle Island	22 July 1986	3	TDR	55	RHAU8623
Triangle Island	22 July 1986	8	TDR	12	RHAU8627
Triangle Island	17 July 1986	3	TDR	60	RHAU8629T
Seabird Rocks	7 Aug. 1986	1	TDR	19	RHAU8609
Seabird Rocks	7 Aug. 1986	1	TDR	12	RHAU8610
Seabird Rocks	7 Aug. 1986	1	TDR	16	RHAU8626
Seabird Rocks	7 Aug. 1986	1	TDR	32	RHAU8629S
Seabird Rocks	24 July 1987	3	MDG	27	
Seabird Rocks	7 Aug. 1987	16	TDR (MDG)[b]	26 (26)[b]	RHAU8705
Seabird Rocks	17 Aug. 1987	17	MDG	40	
Seabird Rocks	4 Aug. 1988	5	TDR (MDG)[b]	46 (49)[b]	RHAU8801
Seabird Rocks	4 Aug. 1988	5	TDR	33	RHAU8802
Cleland Island	9 July 1988	1	TDR (MDG)[b]	36 (36)[b]	RHAU88CL

[a] Codes for individual birds used in Fig. 3.

[b] Both types of gauge were deployed together. Results from MDGs are in parentheses.

TABLE 8. Summary of dive and pause times of Rhinoceros Auklets diving

Site	Date	Mean water depth (m)	No. of dives	Dive (s)		Pause (s)		Dive:pause ratio	
				Mean	SD	Mean	SD	Mean	SD
Adult birds									
Ogden Point, Victoria	4 Dec. 1989	13–24	5	47.0	6.3	14.0	4.7	3.91	2.26
Ogden Point, Victoria	4 Dec. 1989	13–24	10	51.6	6.4	9.0	2.5	6.10	1.79
Ogden Point, Victoria	4 Dec. 1989	13–24	8	44.3	8.9	8.7	2.6	5.49	1.17
Ogden Point, Victoria	7 Dec. 1989	12–25	10	40.9	9.6	13.2	7.7	3.94	2.25
Gordon Head, Victoria	11 July 1992	5–20	11	51.4	5.4	11.5	3.0	4.75	1.2
Gordon Head, Victoria	11 July 1992	5–20	11	42.7	4.7	5.6	1.2	7.89	1.34
Gordon Head, Victoria	11 July 1992	5–20	5	52.8	11.4	7.6	1.8	7.16	1.83
Seabird Rocks	20 June 1992	20–40	5	53.2	5.4	25.8	4.6	2.22	0.55
Seabird Rocks	20 June 1992	15–25	4	36.8	9.2	7.8	3.3	5.26	2.16
Seabird Rocks	20 June 1992	15–25	6	29.1	8.1	4.5	1.7	7.14	3.5
Mean (adults) (10 bouts)			—	45.0	7.9	10.8	6.1	5.39	1.76
Newly fledged juvenile									
Seabird Rocks	4 Aug. 1988	15–25	8	31.1	6.1	13.7	5.1	2.59	1.09

NOTE: Each record is from a single bout of diving by one individual.

On four occasions, birds moving parallel to a breakwater at Ogden Point, Victoria were followed, and the horizontal distance travelled in each dive was estimated from measured markers on the breakwater. The horizontal velocity vector averaged 0.90 $m \cdot s^{-1}$ (SD = 0.31, range 0.29 – 1.37 $m \cdot s^{-1}$, $n = 15$ dives). The water in which the birds were diving was 13–24 m deep, but the vertical vector (i.e., depth) of each dive could not be determined. It seems probable, however, that the mean absolute underwater velocity of Rhinoceros Auklets exceeds 1 $m \cdot s^{-1}$, and that burst speeds of 1.5–2.0 $m \cdot s^{-1}$ could be attained.

On one occasion, from close range (<3 m), we observed two Rhinoceros Auklets feeding on 1-year-old sand lance in a densely packed "ball" in Pachena Bay, Vancouver Island. Both auklets attacked the school from below at a depth of 2–4 m, caught the small fish without any noticeable chase, and swallowed their prey underwater.

Distribution of auklets relative to water depth and fish density

The Rhinoceros Auklets observed on three transect routes indicated no consistent preferences for depth, although few foraged in water <15 m deep (Fig. 5). The distribution of auklets differed significantly from that of available water depths (Kolmogorov–Smirnov test, $P < 0.01$ in each case), but this might simply be a result of the non-uniform distribution of both birds and ocean depths. High auklet densities were found on water with a depth of 21–30 m (Scott Island transect, over a sill at the mouth of Goletas Channel), 31–50 m

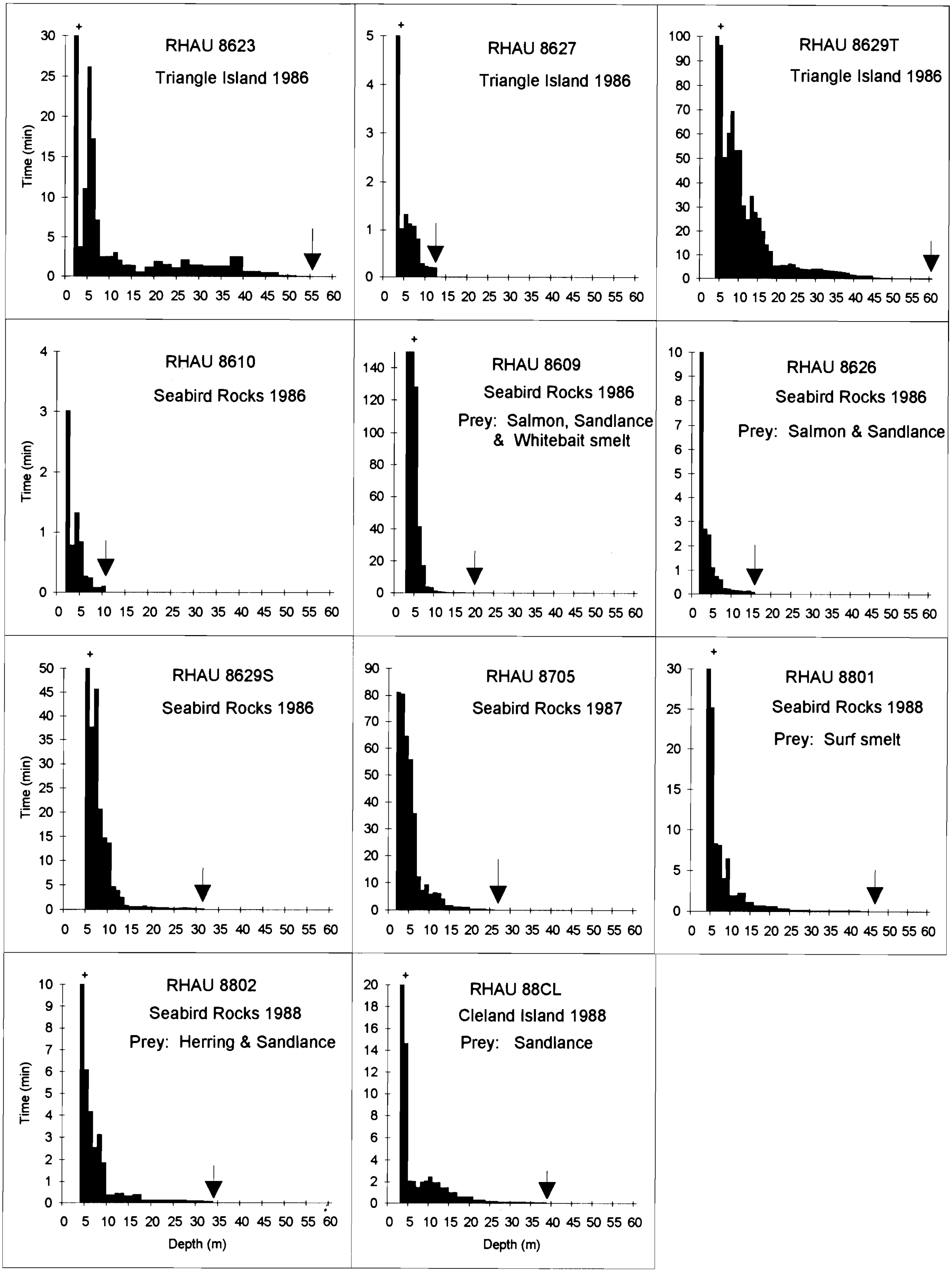

FIG. 3. Results from time-at-depth recorders attached to 11 adult Rhinoceros Auklets. The time (min) in each 1-m depth interval is plotted. The arrow in each graph indicates the greatest depth measured. Prey species being carried by the auklets at the time the gauges were recovered are shown where possible.

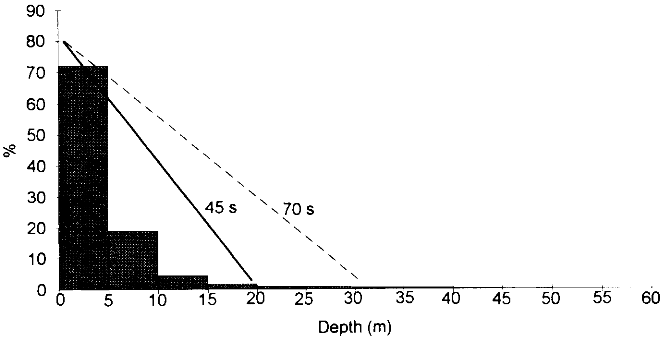

FIG. 4. Histogram showing the mean percentage of time recorded in 5-m depth intervals by time-at-depth recorders from 11 Rhinoceros Auklets (see Fig. 3 for individual traces). The lines represent the percentage of the dive cycle available for foraging at the given depths, as predicted by the efficiency model and assuming dives of 45 and 70 s (aproximately the mean and maximum dive lengths, respectively, recorded in this study; see text for details).

(Barkley Sound), 101 – 160 m (Scott Island transect), or scattered over a wide range of depths (Sidney – Mandarte Island transects).

Discussion

Effects of depth gauges on the birds

It was difficult to assess the effects of capturing, handling, and gauge deployment on the Rhinoceros Auklets. We avoided monitoring the growth and provisioning of chicks in order to minimize disturbance of the tagged birds. We recovered relatively few of the deployed depth gauges, but this appeared to be the result of the small number of opportunities to recapture the tagged birds, avoidance of nets by the birds, or temporary avoidance of the breeding colony by birds that had been handled.

The few studies on the effects of external devices on diving birds give no clear indication of how Rhinoceros Auklets might have been affected. Common Murres (*Uria aalge*) carrying external radio transmitters were reported to have altered time budgets, and slightly reduced food delivery rates (Wanless et al. 1988), but this may have been partly because of the added hindrance of the radio antenna (Croll et al. 1992). Cairns et al. (1987) reported no significant ill effects among murres carrying quite bulky devices. Croll et al. (1992) found some loss of weight among Thick-billed Murres (*Uria lomvia*) fitted with TDRs, and speculated that the devices might have diminished the efficiency of locomotion in air and under water, although most birds behaved in a normal manner.

The hydrodynamic drag of an external device, which is directly proportional to its frontal area (Vogel 1981), is of greater concern than the effects of added mass to the bird (Wilson et al. 1986; Croll et al. 1991*b*). Our largest device, the TDR, had a frontal area about 2.3% of the maximum cross-sectional area of a Rhinoceros Auklet. This is well within the threshold area (6.8%) of devices with which Jackass Penguins (*Spheniscus demersus*) were able to balance their energy budgets at sea (Wilson et al. 1986). A device of this proportion (2.3%) was thought to reduce the underwater velocity of a penguin by 7% (Croll et al. 1991*b*), but it is not known whether alcids respond similarly.

We found no deleterious effects of the gauges on prey delivery to chicks. Birds with gauges caught similar prey species to other birds, and delivered meals that were 93 – 145% of the average mass delivered by unencumbered auklets. One of two birds lost weight (4% of original mass over 16 days), but this rate of weight loss can occur during chick rearing in unencumbered alcids (Croll et al. 1991*a*, 1992). Rhinoceros Auklets routinely catch active prey while carrying loads of fish in their beaks. The TDRs we used were of considerably lower mass (6 g) and bulk than the meals normally delivered to chicks (30 g, range 5.9 – 76.2 g), and therefore probably induced less drag in flight or underwater than did prey held in the beak. Overall, we feel that the TDRs and MDGs did not impose a significant hindrance on the auklets.

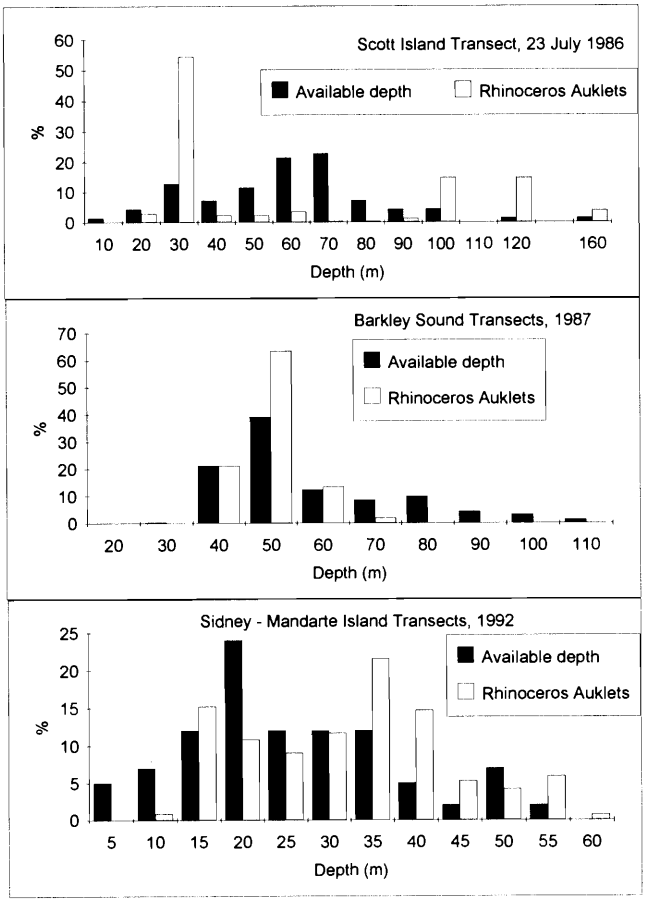

FIG. 5. Distribution of Rhinoceros Auklets at the water surface for various depths of ocean along three transect routes, compared with the frequency of available ocean depths, measured at fixed intervals along the route.

Underwater foraging profiles

Rhinoceros Auklets were capable of diving to 60 m, but all birds with TDRs confined most of their foraging to considerably shallower depths. On average, 90% of time underwater was spent at depths of 0 – 10 m. Our gauges did not record time spent in the upper 2 – 5 m, so this is a conservative estimate. In most cases the birds made a few deep dives, showing that water depth exceeded 10 m and was not the limiting factor. Our transect data supported this conclusion: the auklets avoided shallow water. There was no indication that the auklets were bottom feeders. The shape of their TDR traces was quite different from those associated with bottom feeding (e.g., Wanless et al. 1991).

The two factors most likely to have influenced the diving behaviour of Rhinoceros Auklets were the physiological limitations on their diving abilities, and the distribution and behaviour of their prey. These are discussed below.

Limitations of diving performance

The limitations imposed on diving birds by oxygen requirements have been intensively studied in the laboratory (reviewed by Butler and Jones 1982; Jones and Furilla 1987; Kooyman 1989). The limits of aerobic respiration are set by the volume of oxygen carried in the bird's lungs, air sacs, blood, and tissues as it dives. If the duration of the dive remains within the limits set by aerobic respiration, these oxygen stores can be rapidly restored at the surface between dives and the bird can spend a large proportion of the dive cycle underwater. On average, the Rhinoceros Auklets we observed spent 80% of each dive cycle underwater, and their mean dive:pause ratio (5.39) is comparable to those of other efficient divers (Ainley and Boekelheide 1990). Some diving birds, notably King Penguins, *Aptenodytes patagonicus* (Kooyman et al. 1992) and Thick-billed Murres (Croll et al. 1992) spend an appreciable part of their time underwater at depths at which they must use anaerobic metabolism and hence incur the penalties of lactic acid accumulation. These penalties include increasingly prolonged periods required at the surface to clear the lactate, which could lead to less time spent diving and hence a reduced foraging efficiency. The near-linear relationship between pause and dive times in Rhinoceros Auklets (eq. 2) suggests that most of the observed dives were aerobic, because with prolonged anaerobic diving pause times increase with a power function, rather than linearly (Wilson and Wilson 1988; Ydenberg 1988; Croll et al. 1992).

The oxygen stores and metabolic rates of diving Rhinoceros Auklets are not known, but we applied a simple model of foraging efficiency (Ydenberg and Clark 1989; Burger 1991) to help interpret the observed time-at-depth traces. Foraging efficiency (E) is the proportion of each dive cycle that could be spent foraging at the depths recorded by the TDRs. The dive cycle consists of dive time (T_d) and recovery time at the surface (T_r), with T_d further divided into vertical travel time T_t (down and up) and foraging time T_f. Therefore,

$$[2] \quad E = T_f/(T_f + T_t + T_r)$$

We examined the efficiency of a Rhinoceros Auklet diving with vertical velocity V to feed on a school of fish at depth d. Since T_t ($2d/V$), T_f ($T_d - 2d/V$), and T_r ($0.18\ T_d^{1.06}$; eq. 1) can be expressed as functions of T_d, d, and V, eq. 3 can be rewritten as

$$[3] \quad E = \frac{T_d - 2d/V}{(T_d - 2d/V) + 2d/V + 0.18\ T_d^{1.06}}$$

We assumed that the vertical velocity was similar to the measured horizontal vector (i.e., $0.9\ \mathrm{m \cdot s^{-1}}$), which would be true if the dive angle was 45°. Foraging efficiency E was calculated for dive times of 45 and 70 s (aproximately the mean and maximum dive times we observed), and was compared with the pooled results from the TDRs (Fig. 4). Foraging efficiency declines with depth, and no foraging is predicted at depths of 20 and 31 m for dives of 45 and 70 s, respectively. Foraging at greater depths would require prolonged dives, probably invoking anaerobiosis. Just to reach 60 m in a bounce dive (i.e., no additional time spent at the deepest depth), would require a dive of 133 s (3 × the mean of 45 s). The pooled TDR data indicate that 95% of the auklets' foraging time was spent at depths that could be comfortably reached within the mean dive time, allowing time for foraging (Fig. 4). By remaining within the upper 10 m the auklets ensured that no less than 40% of the average dive cycle could be spent at the selected foraging depth. Foraging at shallow depths incurs the appreciable energetic costs required to counteract buoyancy (Lovvorn and Jones 1991; Wilson et al. 1992), but we have insufficient data to assess these costs relative to the auklet's overall power output.

The angle at which the auklets dive is not known. Birds leaving the surface appeared to dive at about 45°, but studies on other divers have shown that the angle of ascent and descent is likely to be nearer the vertical in deep dives (Wilson and Wilson 1988; Wilson et al. 1993). This would tend to extend the depth of aerobic activity and so support our conclusions that Rhinoceros Auklets very seldom incurred significant anaerobic glycolysis during diving.

Ecology of the prey of Rhinoceros Auklets

The prey composition of our samples was similar to those from other colonies in British Columbia (Vermeer 1979, 1980; Vermeer and Westrheim 1984; Vermeer and Devito 1986; Bertram 1988; Bertram et al. 1991), southeastern Alaska (Hatch 1984), and Washington (Richardson 1961; Wilson and Manuwal 1986). Rhinoceros Auklets took a wide range of prey types, predominantly epipelagic schooling fish. Vermeer (1980) concluded that Rhinoceros Auklets, unlike Tufted Puffins (*Fratercula cirrhata*), were able to breed successfully during periods when sand lance and other preferred species were less available, by switching to alternative prey species. Most meals comprised one species, suggesting that the auklet might have gathered the meal from a single school. In the few samples in which we estimated the sequence of capture, the larger fish appeared to have been caught first, with the meal then completed through the addition of smaller prey. We sometimes observed auklets carrying loads of fish repeatedly diving close to the colonies. It is possible that meals of larger prey might be "topped up" by the addition of smaller prey, such as juvenile rockfish, caught while the adults waited for darkness on the sea near the colony.

The vertical distribution and ecology of some important prey species were reviewed to help interpret the auklet's diving abilities and access to prey. Most prey species spent a significant part of their time foraging near the surface (< 10 m) in nearshore waters. This included first-year herring (Grosse and Hay 1988), newly smolted salmon (Neave et al. 1976), smelt (Hart 1973), and first- and second-year sand lance (Reay 1970; Field 1988). Juvenile herring were most often found at the surface (0–6 m) during dawn and dusk feeding peaks, and at depths of 3–15 m during the rest of the day (Hourston 1959; Hourston and Haegele 1980). They sometimes foraged in mixed schools with juvenile sand lance, which may account for their co-occurrence in the auklet meals. Market squid were relatively insignificant prey for Rhinoceros Auklets in British Columbia and Alaska (Vermeer et al. 1987; Sanger 1987), but occurred in 85% of the auklets sampled off California (Baltz and Morejohn 1977). Schools of squid were commonly found by day at depths of 20–50 m, moving to the surface to feed at night (Bernard 1980; Maupin 1988).

Pacific saury were most abundant in waters 60–200 km offshore (Smith et al. 1970). They were most often encountered near the surface, but may go deeper than 200 m (Hart 1973). This species was delivered to chicks by Rhinoceros Auklets only at colonies on the outer Pacific coast in British Columbia and Washington (Vermeer and Westrheim 1984; Wilson and Manuwal 1986), and was particularly important there when sand lance and juvenile rockfish were apparently less available (Vermeer 1980).

Pacific sand lance were consistently important prey in British Columbia and Washington (Vermeer et al. 1987). Schools of these semi-demersal fish appear to be restricted to water less than 100 m deep (Field 1988). They usually bury themselves in loose sand during part of the day, often at night (Field 1988), and are most vulnerable to fish predators when they enter or emerge from these sandy retreats (Hobson 1986). Our analyses of bite marks and diving depths showed that Rhinoceros Auklets were not catching sand lance in these vulnerable transition periods but tended to catch them from below, near the water surface, during the fish's feeding phase.

Several of the prey species were planktivores that often foraged near the surface in twilight or at night. Crepuscular or nocturnal feeding has been reported in several studies of Rhinoceros Auklets (Vermeer et al. 1987). During our study, we caught two auklets on Cleland Island more than an hour after dark (at 23:14 and 23:24 on 9 July 1988) that were carrying live, freshly caught sand lance. Breeding adults, which spend most of the night hours in their burrows, must, however, do most of their feeding by day, particularly those that forage at some distance from the colony.

Overall, our analysis of prey confirmed that Rhinoceros Auklets breeding at three colonies in British Columbia were primarily feeding in the epipelagic zone, and usually captured small fish by diving below schools in the upper and midwater zone. Rhinoceros Auklets are known to herd small fish, including sand lance, towards the ocean surface (Grover and Olla 1983). We did not examine the diets of adult birds, but they also appear to eat epipelagic fish and squid (Vermeer et al. 1987).

Implications for monitoring prey availability

Rhinoceros Auklets frequently feed in water far deeper than their usual diving range, often seaward of the shelf break (Wahl 1975; Briggs et al. 1987; Ainley and Boekelheide 1990; Morgan et al. 1991). Efficient foraging for the auklets is restricted to the upper 20–30 m, and prey below 60 m might be inaccessible. Unfavourable oceanic conditions, such as El Niño events, or reduced upwelling, may cause fish to remain in deep water, perhaps out of range. Sand lance, for example, are known to become dormant, buried in sand, with high sea temperatures (above 20°C in *A. personatus*; Field 1988). Dietary changes and reduced breeding success associated with reduced predation on sand lance (Vermeer 1980; Vermeer and Westrheim 1984; Bertram et al. 1991) or anchovies (Wilson and Manuwal 1986) might be due to the inaccessibility of the prey rather than to reduced abundance.

Our findings have important implications for considering diving seabirds as indicators of fish abundance and oceanic change (Vermeer and Westrheim 1984; Bertram 1988; Bertram et al. 1991; Hatch and Sanger 1992). Rhinoceros Auklets respond to prey availability in the upper 20–60 m, rather than the entire water column, which might restrict the scope of any proposed monitoring system to epipelagic waters. On the other hand, the auklets might be sensitive indicators of oceanic processes that keep preferred prey deeper than their diving range. In either event, we need to know a lot more about the bird's foraging activities, and the ecology of their prey.

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Appendix

TABLE A1. Species composition of meals delivered to Rhinoceros Auklet chicks. In many cases, when several birds were caught simultaneously, the meals they were carrying were mixed together. The number of individual fish counted and weighed is therefore far larger than the number in discrete meals

Prey species	% occurrence	Total no. (%)	% of total mass	Item mass (g) Mean	Item mass (g) SD
		Triangle Island (12 – 23 July 1986)			
Loligo opalescens	3.7	4 (1)	1.0	5.8	6.3
Onchorhynchus keta	1.2	3 (1)	1.2	9.3	2.5
Onchorhynchus sp.	8.5	11 (2)	6.1	13.5	5.4
Cololabis saura	25.6	28 (6)	28.7	24.6	4.6
Ammodytes hexapterus	46.3	143 (29)	42.0	7.2	5.0
Sebastes sp.	62.2	255 (53)	17.0	1.6	0.4
Hexagrammos decagrammus	23.2	41 (8)	4.0	2.4	1.2
Flounder sp.	1.2	1 (0.2)	0.1	0.5	—
Sample size	82 (meals)	485 (items)	2397 (g)		
		Seabird Rocks (6 – 20 Aug. 1986)			
Loligo opalescens	7.7	2 (3)	1.6	11.4	—
Clupea harengus	3.1	20 (26)	15.0	5.4	7
Engraulis mordax	15.4	3 (4)	5.1	12.3	7.9
Onchorhynchus sp.	30.8	8 (10)	17.2	15.5	7
Allosmerus elongatus	7.7	1 (1)	0.6	4.6	—
Hypomesus pretiosus	38.5	6 (8)	22.2	26.7	2.9
Trichodon trichodon	7.7	1 (1)	8.6	7.8	—
Ammodytes hexapterus	38.5	35 (45)	29.1	6	2.2
Sebastes sp.	7.7	1 (1)	0.2	1.2	—
Hexagrammos decagrammus	7.7	1 (1)	0.5	3.6	—
Sample size	13 (meals)	78 (items)	722.4 (g)		
		Seabird Rocks (22 July – 17 Aug. 1987)			
Clupea harengus	36.8	31 (15)	12.5	5.6	5.3
Onchorhynchus tsawytscha	15.8	14 (7)	12.3	10.2	3.4
Onchorhynchus keta	5.3	3 (1)	3.3	12.7	1.1
Onchorhynchus kisutch	5.3	2 (2)	2.6	15.0	5.7
Allosmerus elongatus	5.3	1 (0.5)	0.8	9.5	—
Hypomesus pretiosus	15.8	13 (6)	21.9	21.2	14.6
Trichodon trichodon	5.3	1 (0.5)	0.6	7.0	—
Ammodytes hexapterus	52.6	144 (69)	45.9	3.7	2.3
Sample size	19 (meals)	209 (items)	1160 (g)		
		Seabird Rocks (26 July – 4 Aug. 1988)			
Clupea harengus	47.6	49 (58)	33.2	4.9	4.4
Onchorhynchus keta	14.3	6 (7)	11.6	13.4	2.2
Allosmerus elongatus	14.3	4 (5)	4.3	7.4	1.7
Hypomesus pretiosus	4.7	9 (10)	41.4	31.8	7.1
Ammodytes hexapterus	23.8	17 (20)	9.5	3.9	1.5
Sample size	21 (meals)	85 (items)	692 (g)		

Appendix *(concluded)*

Prey species	% occurrence	Total no. (%)	% of total mass	Item mass (g)	
				Mean	SD
		Seabird Rocks (24 June 1989)			
Onchorhynchus sp.	*	1 (5)	18.4	9.5	—
Allosmerus elongatus	*	4 (20)	30.2	3.9	0.5
Ammodytes hexapterus	*	14 (70)	44.7	1.7	0.6
Hexagrammos decagrammus	*	1 (5)	6.8	3.5	—
Sample size	Not recorded	20 (items)	52 (g)		
		Cleland Island (7–9 July 1988)			
Clupea harengus	8.3	4 (2)	0.6	1.8	0.3
Ammodytes hexapterus	97.2	243 (93)	95.8	3.7	2.0
Sebastes sp.	16.6	12 (5)	3.6	2.8	1.2
Sample size	36 (meals)	260 (items)	936 (g)		