Diving depths and diet of Cassin's Auklet at Reef Island, British Columbia

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Diving depths of Cassin's Auklets (*Ptychoramphus aleuticus*) breeding at Reef Island, Queen Charlotte Islands, British Columbia, were measured with miniature gauges attached to the birds. Maximum diving depths of 22 birds averaged 28 m, with a mode of 40 m. A time-at-depth recorder showed that one auklet dived to 29 m, but spent 80% of its time underwater at 3–13 m. Food delivered in gular pouches to chicks contained mainly euphausiids (predominantly *Thysanoessa spinifera*) and juvenile fish (*Ammodytes hexapterus*), with lesser amounts of copepods, amphipods, small pandalid shrimps, Brachyura larvae, and ctenophores. Euphausiid meals were most common during spring tides. Auklets that delivered significant amounts of euphausiids appeared to have dived deeper than those that delivered fish.

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La profondeur de plongée a été enregistrée au moyen de minisenseurs attachés à des alques de Cassin (*Ptychoramphus aleuticus*) réunis pour la reproduction dans l'île Reef des îles de la Reine-Charlotte, Colombie-Britannique. La profondeur maximale enregistrée au cours des plongées de 22 oiseaux était en moyenne de 28 m (mode de 40 m). Un appareil permettant d'enregistrer à la fois le temps en relation avec la profondeur a révélé qu'un oiseau avait plongé jusqu'à 29 m, mais avait passé 80 % de son temps sous l'eau entre 3 et 13 m. La nourriture apportée aux oisillons dans les poches gulaires était composée en grande partie d'euphausiacés (surtout *Thysanoessa spinifera*) et de poissons immatures (*Ammodytes hexapterus*), mais contenait aussi, en moins grande quantité, des copépodes, des amphipodes, des petites crevettes pandalides, des larves de brachyoures et des cténophores. Les repas d'euphausiacés étaient plus fréquents durant les marées de printemps. Les alques qui rapportaient des quantités importantes d'euphausiacés semblaient avoir effectué des plongées plus profondes que les alques qui rapportaient du poisson.

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Introduction

Cassin's Auklets (*Ptychoramphus aleuticus*), like many other alcid seabirds, spend most of their time at sea, out of sight of land-based observers. Consequently, little is known about their foraging behavior, particularly when diving underwater (Vermeer et al. 1987*a*). During the breeding season, the auklets forage offshore, over the continental shelf and shelf edge (Gould et al. 1982; Vermeer et al. 1985; Sanger 1987). The diets of adults and chicks are similar (Vermeer et al. 1985), but there is significant geographical variation in diet and the birds have been studied at relatively few locations (see Vermeer et al. 1987*a* for a review). In general, Cassin's Auklets eat zooplankton, with euphausiids and calanoid copepods being dominant and other crustaceans, juvenile fish, and squid less frequent (Vermeer 1985; Vermeer et al. 1987*a*).

We used a maximum-depth gauge (hereafter MDG, Burger and Wilson 1988) to record maximum diving depths, and a time-at-depth recorder (hereafter TDR, Wilson et al. 1989) to provide a profile of underwater foraging activity of Cassin's Auklets in British Columbia. In addition, we collected meals destined for Cassin's Auklet chicks, to provide data on the geographical variation of prey. These data provide new insights into the diving capabilities and foraging niche of Cassin's Auklets. This is one of the most abundant seabirds breeding in the northeast Pacific, but the relationships between its diet and diving depths are not known.

Methods

The study was made at Reef Island (52°52′N, 131°31′W), one of the eastern Queen Charlotte Islands, in Hecate Strait, British Columbia.

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Adult auklets were trapped, as they returned to their nests, using mist nets and tubular, trap-door burrow traps. All captured birds were banded, and a sample of breeding adults was fitted with one of the two depth gauges. MDGs consisted of 8 cm lengths of plastic tubing (Tygon brand; internal diameter, 1.6 mm) lined with 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). Upon recovery the MDGs were inspected. Those showing damage or internal moisture buildup, and those that had been deployed for over 6 days, were rejected (see Burger and Wilson 1988).

The TDRs were constructed from 3-cm^3 disposable syringes, and photographic film (Kodak Pan-X developed in Microdol) was used to record the depth-dependent position of a light-emitting diode. Wilson et al. (1989) describe the gauge in detail. 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 slit width set at 0.3 mm. Time and depth calibrations were made by lowering the 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 the film, and the error resulting from light spreading was reduced using a deconvolution procedure outlined by Wilson et al. (1989) and with the aid of a computer program provided by C. Nöldeke and R. P. Wilson (Institut für Meereskunde, Universität Kiel, Kiel, Federal Republic of Germany).

Our MDGs weighed <1 g, which was <0.06% of the mass of the adult bird (188 g, Vermeer et al. 1985), and had a cross-sectional area (13 mm^2) about 0.5% of that of the adult bird in mid-body (2827 mm^2, measured on a dead adult). Corresponding values for our TDRs were 6 g (3% of the adult's mass) and 153 mm^2 (5.4% of the adult's area). Each gauge was taped to a few of the bird's dorsal feathers with a strip of Superstik waterproof adhesive tape, with the tape smoothed down to minimize drag on the bird (Wilson and Wilson 1989). Gauges could be removed from recaptured birds without loss of feathers, and those on birds not recaptured would fall off when the tape became less adhesive or the bird molted. MDGs were fixed to feathers on the back or the tail, but TDRs were attached only on the backs of auklets, on the

midline just posterior to the wings. Some tape used in 1988 proved to be defective, and some gauges fell off prematurely.

Food samples were collected from the gular pouches of adults returning to feed chicks. In many instances, birds caught in nets regurgitated the food over a wide area before it could be collected, and hence, relatively few complete meals were obtained. When meals could not be collected, the dominant prey type was determined by careful inspection in the field. Relatively complete meals were preserved in 10% Formalin and the occurrence and volume of each prey type were estimated later. Vertebrae and other fragments of fish were compared with identified reference material from fish caught in nets (specimens courtesy of the Pacific Biological Station, Nanaimo, British Columbia).

Results

Cassin's Auklets were readily trapped with mist nets or burrow traps, but birds that had been handled were more wary and were seen to avoid both traps and nets. Recapture success of birds fitted with MDGs (omitting multiple recaptures) was similar when using mist nets only (27%, $n = 118$) burrow traps (27%, $n = 15$), or a sequential combination of burrow traps and mist nets (33%, $n = 9$). The recapture success was similar among birds fitted with MDGs (35%), TDRs (39%), or no gauges (38%, Table 1). MDGs fitted to the rectrices, or those attached to the back with defective tape in 1988, were frequently lost, but no MDGs were lost off the birds' backs in 1987. The birds lost the TDRs more frequently than MDGs (Table 1).

Thirty of the 129 MDGs deployed were recovered and 22 were intact and without visible sources of error. These indicated maximum depths averaging 28 m ± 12 SD, with a mode of 40 m and a range of 6–43 m (Table 2). Only one time-at-depth trace was obtained (Fig. 1). This bird had dived briefly to a maximum depth of 29 m, but 80% of its time underwater was spent at 3–13 m below the surface. Its gular pouch contained fragments of fish.

Fish and euphausiids constituted the bulk of most of the meals analyzed in detail, but copepods, amphipods, pandalid shrimps, crab larvae, and ctenophores were also present (Table 3). *Thysanoessa spinifera* and *Euphausia pacifica* were the only euphausiids to be conclusively identified. Many euphausiids were immature and these might have included *Thysanoessa longipes* and *T. spinifera*. Nearly all fish meals had been broken up, and fragments of vertebrae were usually the only identifiable material. Small sand lance *Ammodytes hexapterus* occurred in 100% of the samples that contained identifiable fish material ($n = 6$ in 1987 and 37 in 1988); no other fish species were found. The fragments of sand lance matched samples of post-larval immature fish, 34–45 mm long, netted in June in Hecate Strait.

Cassin's Auklets rarely mixed prey within a meal; 79% of 58 meals from both years contained only one major prey type (>90%, by volume, of each meal), either fish (56.9%), euphausiids (20.7%), or pandalid shrimps (1.7%). Mixed meals contained fish and crustaceans (12.1%) or a mixture of crustacean species (8.6%). Meal composition changed during the chick-rearing period. In 1987, copepods occurred in visually inspected meals between 18 and 21 May but not later, and in both years, euphausiids became more prominant in the latter half of the sampling period. The periods when euphausiid meals were common coincided with maximum tidal range (Table 4; tide levels from the Canadian Hydrographic Service, 1987 and 1988 tide charts for Bella Bella, British Columbia).

Diving depths were also related to prey types and tidal ranges. With data from both years pooled, the maximum diving depths during neap tides were significantly shallower than those

TABLE 1. Recapture rates of Cassin's Auklets fitted with maximum-depth gauges (MDGs), time-at-depth recorders (TDRs), or no gauges, and numbers of gauges recovered

Type of gauge and attachment	Year	No. of birds caught*	Birds recaptured*		Gauges recovered*	
			No.	%	No.	%
MDG on tail	1987	27	13	48	3	11
MDG on back	1987	39	16	41	16	41
	1988	63	16	25	11	17
Total		129	45	35	30	23
TDR on back	1987	17	6	35	2	12
	1988	14	6	43	0	0
Total		31	12	39	2	6
No gauges	1987	47	20	43	—	
	1988	5	0	0	—	
Total		52	20	38	—	

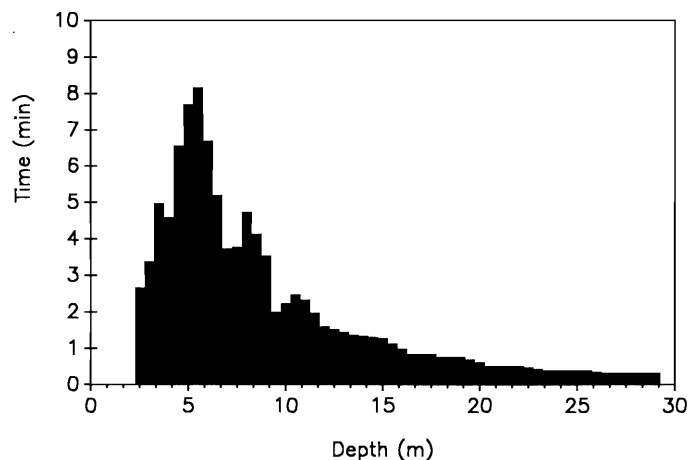*These include birds recaptured and refitted with new gauges.

FIG. 1. Time spent at various depths by a Cassin's Auklet recaptured on Reef Island on 5 June 1987, 1 day after the time-at-depth recorder was attached. The gauge began to record at depths below 2.8 m.

measured during spring tides (Table 5, Mann–Whitney test, $U_{13,9} = 101.7$, $P < 0.01$). In addition, the mean maximum depth attained by auklets carrying predominantly fish (22 m ± 11 SD, $n = 10$) was significantly shallower than the mean depth of birds carrying euphausiids or euphausiid–fish mixtures (33 m ± 12 SD, $n = 9$; Mann–Whitney test, $U_{10,9} = 69.3$ $P < 0.05$; Table 2). It appears that euphausiid meals were associated with deep dives during spring tides, but our samples were inadequate to test this more rigorously within each year.

Discussion

Recapture success and the effects of the gauges

A major limitation in the use of activity recorders attached to free-living seabirds is the difficulty in recovering the devices with minimal disturbance (Burger and Simpson 1986). Mist nets, used alone or in combination with burrow traps, were effective in our study, although the Cassin's Auklets, having excellent night vision, learned to avoid them. Waterproof tape is a suitable method for attaching small devices to seabirds (Wilson and Wilson 1989), but many TDRs and a few MDGs were lost when the few feathers to which they were taped pulled out.

TABLE 2. Maximum depths recorded for Cassin's Auklets at Reef Island in 1987 and 1988, and the type of prey being carried in the gular pouch

Band number	Date recovered	No. days deployed	Depth (m)	Principal prey in gular pouch (% volume where known)
			1987	
912	21 May	3	20	Fish
128	27 May	2	21	Fish
130	29 May	3	35	Fish
010	5 June	1	18	No food collected
129	13 June	2	38	Euphausiids
184	13 June	2	35	Fish + euphausiids
192	13 June	2	40	Fish
129[a]	14 June	1	40	No food collected
184[a]	14 June	1	40	Fish + euphausiids
192[a]	14 June	1	35	No food collected
196	14 June	1	40	Euphausiids
188	16 June	5	43	Euphausiids
195	16 June	3	40	Euphausiids
			1988	
180	24 May	3	20	Fish (100)
219	25 May	2	18	Fish (90), euphausiids (10)
240	25 May	2	9	Euphausiids (99)
180[a]	27 May	3	15	Fish (95), euphausiids (5)
129	27 May	3	10	Fish (95), euphausiids (5)
210	28 May	3	19	Fish (40), mixed crustaceans (60)
189	30 May	3	6	Fish (100)
219[a]	31 May	6	36	Euphausiids (95), fish (5)
983	2 June	3	30	Fish (100)

[a]Birds recaptured twice, with refitted gauges.

The effects of the devices on the auklets are of concern. Common Murres (*Uria aalge*) which were carrying external radios were reported to have altered time budgets and slightly reduced food delivery rates (Wanless et al. 1988), but Cairns et al. (1987) reported no significant ill effects among murres carrying quite bulky devices. The effects of devices on other alcids have not been reported. Wilson et al. (1986) showed that the disruption of underwater streamlining of penguins was of greater concern than the effects of the mass of the device. Wilson et al. (1986) found that penguins could maintain a balanced energy budget while fitted with devices having cross-sectional areas <6.8% of the bird's mid-body cross-sectional area. This is proportionately larger than both of our devices (MDGs and TDRs were 0.5 and 5.4% of the auklet's cross-sectional area, respectively).

Both gauges weighed substantially less than the mean mass of food carried by Cassin's Auklets to the chicks (28 g in California, Manuwal 1974; 19 g in British Columbia, Vermeer et al. 1985). The MDGs appeared to have no more effect on the birds than normal banding procedures, judging by the comparable rate of recapture and the apparently normal delivery of food to chicks. Birds carrying the TDRs were recaptured with similar frequency, but often after the device had been lost or pulled off. It seems likely that these larger devices were more irritating to birds than MDGs.

Diving depths, diet, and underwater foraging niche

Cassin's Auklets from Reef Island regularly dived to 40 m, and occasionally deeper. Using similar MDGs, D. Croll and H. Carter (personal communication) recorded similar depths among Cassin's Auklets breeding on southeast Farallon Island, California ($\bar{x}$ = 32 m ± 7 SD, n = 5, range = 24–39 m).

Dolphin and McSweeney (1983) surmised indirectly that Cassin's Auklets were feeding on euphausiid patches 27–35 m deep. Maximum diving depths in alcids are correlated with body mass (Piatt and Nettleship 1985; Prince and Harris 1988), and the maximum depths attained by Cassin's Auklets lie close to the value predicted by an allometric regression for wing-propelled diving birds (45 m; Burger 1990).

The time-at-depth trace produced here is the first to be published for any alcid. The Cassin's Auklet spent 80% of its time underwater at depths of 3–13 m, but very little time near the maximum depth possible. The vertical velocity of diving and ascending is not known for Cassin's Auklet, but is probably about 1.2 m·s^{-1} (Burger 1990). They remain underwater for 45–60 s (Thoresen 1964). These estimates allow the proportion of time spent foraging (searching for and capturing prey) and vertical travelling to be estimated for various depths. During 50-s dives, an auklet could spend 90 and 57% of each dive foraging when diving to 3 and 13 m, respectively, but would have no time for foraging at 30 m. Our preliminary interpretation of the time-at-depth trace is that deep dives were exploratory to seek concentrations of prey, but that most foraging occurred at relatively shallow prey patches, allowing a large proportion of each dive to be spent capturing the small prey items.

Many more time-at-depth results are required to compare underwater niches of diving birds and to test the hypothesis that diving ability affects resource partitioning and coexistence in alcids (Cody 1973; Bédard 1976; Piatt and Nettleship 1985). Depth gauges have provided significant new insights into the foraging strategies of penguins (Kooyman et al. 1982; Wilson 1985) and fur seals (Gentry and Kooyman 1986).

Euphausiids, particularly *T. spinifera*, were dominant in

Table 3. Percentage occurrence and percentage volume of prey types sampled from gular pouches of Cassin's Auklets at Reef Island

Prey type	1987 (n = 13)[a]		1988 (n = 45)[b]	
	Occurrence	Volume	Occurrence	Volume
Euphausiacea				
Thysanoessa sp.	15.4	7.8	31.1	13.8
T. spinifera	92.3	21.2	26.7	8.5
Euphausia pacifica	23.1	3.1	11.1	1.2
Unidentified	7.7	Trace	2.2	Trace
Total	100.0	32.1	57.8	23.6
Calanoida				
Neocalanus sp.	7.7	3.8	0	0
Amphipoda				
Parathemisto sp.	23.1	3.9	4.4	0.5
Gammarids	30.8	10.0	0	0
Euprimno sp.	0	0	2.2	Trace
Unidentified	0	0	2.2	Trace
Total	30.8	13.9	8.9	0.6
Caridea				
Pandalid shrimps	23.1	2.0	28.9	7.7
Brachyura larvae				
Cancer magister				
Zoea	0	0	4.4	0.1
Megalops	7.7	Trace	0	0
C. oregonensis				
Megalops	7.7	Trace	2.2	Trace
Unidentified	0	0	4.4	0.1
Total	15.4	<0.2	8.9	0.2
Ctenophores				
Pleurobrachia sp.	0	0	2.2	Trace
Pisces				
Ammodytes hexapterus	46.2	—	82.2	—
Total[c]	53.8	48.7	88.9	67.9

[a]Sampling dates were 19 May to 13 June.
[b]Sampling dates were 21 May to 14 June.
[c]Not all fish material could be identified, but immature Ammodytes hexaterus was the only species found.

Table 4. Frequency of meals dominated by euphausiids during spring and neap tides

Year	Tide	Date	Daily maximum tidal range (m)*		Occurrence of meals dominated by euphausiids	
			Mean	Range	%	n
1987	Neap	25 May–8 June	3.2	2.2–4.2	16	32
	Spring	10–15 June	4.8	4.5–5.2	61	31
1988	Neap	21–27 May	2.4	2.1–2.9	10	30
	Spring	28 May–1 June	4.1	3.4–4.6	43	14

*The difference between the lowest low and the highest high tide for each day.

many of our samples, a trend also found for Cassin's Auklets in California (Thoresen 1964; Manuwal 1974; Speich and Manuwal 1974), and in some samples from British Columbia (Vermeer 1981; Vermeer et al. 1985). Copepods were major food items at Frederick Island, one of the northwestern Queen Charlotte Islands (Vermeer et al. 1985, 1987a), and in the Gulf of Alaska (Sanger 1987), but were rare in our samples from Reef Island. Conversely, fish, a major component in our samples, were present but uncommon in meals of Cassin's Auklets from other parts of British Columbia (Vermeer 1981; Vermeer et al. 1985, 1987a) and the Gulf of Alaska (Sanger 1987). Small sand lance (45–60 mm in length) were commonly eaten by other alcids and some surface-feeding seabirds off British Columbia (Sealy 1973, 1975). Immature lanceolate fish were common in Thoresen's (1964) samples from the Farallon Islands, California, but not in Manuwal's (1974) samples from the same islands. The differences between our samples and others from British Columbia might simply reflect the inadequate sampling

TABLE 5. Relationships between maximum diving depths and diet of Cassin's Auklets during neap and spring tides

Major component of meals	Maximum depth (m)	
	Neap tides	Spring tides
Fish	20±8 (7)	25±17 (3)
Euphausiids	9 (1)	39±3 (5)
Euphausiids and fish	—	31±11 (3)
No meals collected	18 (1)	38±4 (2)
Total	18±8 (9)	34±10 (13)

NOTE: Periods of neap and spring tides as specified in Table 4. Means ± SD and sample size (in parentheses) are given with data from 1987 and 1988 combined.

effort in this region. Alternatively, the diets might differ because of differences in bottom topography, depth, water stratification (Thomson 1981), and plankton communities (Fulton et al. 1982) between the waters of Hecate Strait and other, more exposed coastal regions.

The temporal changes in diet and associated maximum diving depths are difficult to interpret, given the paucity of data on the biology and distribution of euphausiids and sand lance in Hecate Strait. Euphausiids, including *T. spinifera*, and other large plankton tend to remain in deeper waters (>200 m) off the Queen Charlotte Islands during daylight, although concentrations do occur in shallower water as spring progresses (Fulton et al. 1982; Fulton and LeBrasseur 1984), and *T. spinifera* may at times be an important prey for surface-feeding birds off the Queen Charlotte Islands (Sealy 1973, 1975). Daytime surface aggregations are sometimes related to breeding activity in euphausiids, including *T. spinifera* (Smith and Adams 1988), but we found few gravid euphausiids in our samples and many immature animals. Strong advective tidal currents bring euphausiids and other plankton to the surface, where they become available to seabirds (Brown et al. 1979; Vermeer et al. 1987b; Mackas and Fulton 1989). This might also have occurred in Hecate Strait, since euphausiid meals were most common during spring tides, when maximum tidal flow and thus strong advective currents occurred.

Immature sand lance of the 0-year age-class appeared to be readily available to Cassin's Auklets at relatively shallow depths. Sand lance of this size (30–60 mm in length) were common in a mid-water trawl made in Queen Charlotte Strait in June (Westrheim and Harling 1983) and were important prey for fish (Westrheim and Harling 1983) and seabirds (Sealy 1973, 1975) off the Queen Charlotte Islands. In the North Atlantic, the larvae of *Ammodytes* spp. tend to be concentrated in surface water within 20–30 m, but the post-larval juveniles are more widely dispersed (Reay 1970). The life history of sand lance in Hecate Strait is poorly understood. Our data indicate that combined analyses of the diets and diving activities of seabirds will provide useful data on commercially important, but poorly known prey species, such as sand lance.

Cassin's Auklets are restricted to the upper 30–40 m of the ocean, but generally aggregate on water much deeper than that (Vermeer et al. 1985). Since the birds return to the colonies at night, we assume that most foraging occurs during daylight, when the greatest concentrations of their zooplankton prey occur below the birds' diving range. Given these conditions, we

postulate that diving limitations strongly affect the oceanic distribution and the chronology and success of breeding in Cassin's Auklets.

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