of their circadian cycle) was intermediate between the predicted values for ratites and nonpasserine carinate birds. It is important to recognize that many factors other than phylogeny (e.g., phase of circadian cycle, season, latitude—see Weathers 1979) can influence basal metabolic rate, so the intermediate basal $\dot{V}O_2$ of tinamous should not be interpreted as conclusive evidence for their being phylogenetically intermediate between ratites and carinate nonpasserines. Nevertheless, the intermediate basal $\dot{V}O_2$ of tinamous is consistent with the phyletically-correlated differences in basal $\dot{V}O_2$ of ratites and carinate nonpasserines (Calder and Dawson 1978, Withers 1983) and the phylogenetic position of tinamous as nonratite but palaeognathous carinates (Cracraft 1981).

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LITERATURE CITED

Aschoff, J. 1981. Thermal conductance in mammals and birds: its dependence on body size and circadian phase. Comp. Biochem. Physiol. A. Comp. Physiol. 69:611–619.

Aschoff, J., and H. Pohl. 1970. Rhythmic variations in energy metabolism. Fed. Proc. 29:1541–1552.

Calder, W. A., and T. J. Dawson. 1978. Resting metabolic rates of ratite birds: the Kiwis and the Emu. Comp. Biochem. Physiol. A. Comp. Physiol. 60:479–481.

Cracraft, J. 1981. Toward a phylogenetic classification of the recent birds of the world (Class Aves). Auk 98:681–714.

Crawford, E. C., and R. C. Lasiewski. 1968. Oxygen consumption and respiratory evaporation of the Emu and Rhea. Condor 70:333–339.

Crawford, E. C., and K. Schmidt-Nielsen. 1967. Temperature regulation and evaporative cooling in the ostrich. Am. J. Physiol. 212:347–353.

Farner, D. S., N. Chivevs, and T. Riney. 1956. The body temperature of North Island Kiwis. Emu 56: 199–206.

King, J. R., and D. S. Farner. 1961. Energy metabolism, thermoregulation and body temperature. *In* A. J. Marshall [ed.], Biology and comparative physiology of birds. Vol. 2. Academic Press, New York.

Parrish, O. O., and T. W. Putnam. 1977. Equations for the determination of humidity from dew-point and psychrometric data. NASA Tech. Note D-8401.

Weathers, W. W. 1979. Climatic adaptation in avian standard metabolic rate. Oecologia 42:81–89.

Withers, P. C. 1977. Measurement of $\dot{V}O_2$, $\dot{V}CO_2$ and evaporative water loss with a flow-through mask. J. Appl. Physiol. Resp. Environ. Exercise Physiol. 42:120–123.

Withers, P. C. 1983. Energy, water and solute balance of the ostrich *Struthio camelus*. Physiol. Zool. 56:568–579.

Zar, J. H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, NJ.

The Condor 89:426–430

WINTER DIETS OF COMMON MURRES AND MARBLED MURRELETS IN KACHEMAK BAY, ALASKA[1]

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Key words: Common Murre; Marbled Murrelet; foraging habitat; mysids; euphausiids; pandalid shrimp; capelin; Pacific sand lance.

Knowledge of the winter diets of seabirds in high latitudes like Alaskan waters has been an elusive aspect of their biology. Scanty information on winter diets of Common Murres (*Uria aalge*) are available from the Pribilof Islands (Preble and McAtee 1923), California (Baltz and Morejohn 1977), Kodiak Island (Krasnow and Sanger 1986), Newfoundland (Tuck 1960) and the North Sea (Blake 1984), and for Marbled Murrelets (*Brachyramphus marmoratus*) from British Columbia (Munro and Clemens 1931, Carter 1984) and Kodiak (Krasnow and Sanger 1986). This paper summarizes the diets of these two species, as observed during the winter season of 1977–1978 in Kachemak Bay, Alaska, as a part of the Alaskan Outer Continental Shelf Environmental Assessment Program, OCSEAP (Sanger and Jones 1982; Krasnow and Sanger 1986; Fukuyama, Sanger, and Hironaka, unpubl.) and provides further interpretation of the data.

STUDY AREA

Kachemak Bay (Fig. 1) is a highly productive embayment located near the mouth of Cook Inlet in the ex-

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treme north of the Gulf of Alaska. During this study, air temperature ranged from −13°C in December to 4°C in April and surface water temperatures generally ranged from 4 to 5°C. Both Common Murres and Marbled Murrelets overwinter in the area (Erikson 1977), and the Common Murre is believed to be the most abundant alcid. During this study, Marbled Murrelets were the second most common alcid and Pigeon Guillemots (*Cepphus columba*) occasionally occurred close to shore, but no other alcids were seen. Murrelets and most murres occurred in the southern, deep, ice-free part of the bay.

METHODS

A 5-m open skiff was used to observe and collect birds between 10:00 to 15:00 during monthly field trips of three to five days, between December 1977 and April 1978. Birds were seen and shot within the areas shown in Figure 1. Five to nine murres were collected during each trip, for a total of 31, and beginning in January, five or six murrelets were shot monthly, for a total of 21. Buffered 10% formalin was injected into the stomachs through the esophagus and specimens were frozen.

The esophagus, proventriculus, and gizzard were removed from thawed specimens and stored in 50% isopropanol until their analyses. Stomach contents were

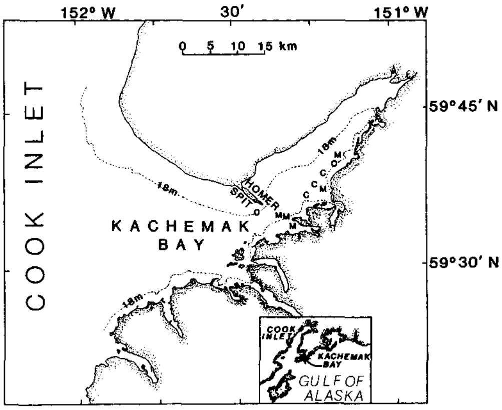

FIGURE 1. Locations where Common Murres (C) and Marbled Murrelets (M) were observed and collected at Kachemak Bay, Alaska. No murres or murrelets were seen on the shallow, north side of the Bay where sea ducks were studied as part of the same general project (Sanger and Jones 1984).

TABLE 1. Winter diet of Common Murres in Kachemak Bay, Alaska between December 1977 and April 1978. $n = 28$ stomachs with food; three other birds had empty stomachs.

Prey	% Nos. Totals: ($n = 385$)	% Vol. (352 ml)	% FO[a]	IRI	% Total IRI	Length data (mm) n	$\bar{x}$	SD	Min	Max
Polychaete worm										
Unidentified nereid	0.3	0.0	3.6	1	0.1					
Crustaceans										
Unidentified	1.1	2.2	14.3	46	0.8					
Mysid										
Neomysis rayii	83.3	49.0	39.3	5,200	85.8	162	34	5.0	31	44
Shrimp										
Eualus sp.	0.3	0.6	3.6	3	0.1					
Pandalus borealis	5.6	16.7	17.9	398	6.6	9	54	7.3	52	79
Pandalus goniuris	0.3	0.4	3.6	2	0.1					
Pandalus spp.	0.3	1.4	3.6	6	0.1					
Unidentified pandalid	0.8	3.9	10.7	51	0.8					
Crangon franciscorum	0.8	3.9	10.7	50	0.8	2	75	7.1	78	86
Crangon spp.	0.3	1.1	3.6	5	0.1					
Unidentified	0.8	3.9	10.7	51	0.8					
Fish										
Unidentified	1.3	1.1	17.9	42	0.7					
Clupea harengus	0.3	5.3	3.6	20	0.3					
Mallotus villosus	0.5	2.5	7.1	22	0.4	1	82	—	—	—
Osmeridae	1.8	0.8	14.3	37	0.6					
Theragra chalcogramma	1.3	5.2	17.9	117	1.9	6	140	21.7	110	175
Unidentified gadid	0.3	0.1	3.6	1	0.1					
Lumpenus maculatus	0.3	1.3	3.6	5	0.1	1	100	—	—	—
Unidentified stichaeid	0.3	0.6	3.6	1	0.1					
Ammodytes hexapterus	0.3	0.1	3.6	3	0.1					

[a] %FO = % frequency of occurrence.

drained, weighed to the nearest 0.1 g, and their total volume measured to the nearest ml by water displacement. Prey items were counted and identified to the lowest possible taxon, and the volume of each was estimated visually as a percent of the total. Total lengths of whole specimens were measured to the nearest mm. Fish otoliths (Frost and Lowry 1981), vertebral columns, and parasphenoid bones of capelin and sand lance were measured to the nearest 0.1 mm for extrapolation to whole lengths (Sanger, Hironaka, and Fukuyama, unpubl.).

Diets for both species, based on pooled data, were calculated in aggregate percent volume (%V, cf. Martin et al. 1946, Swanson et al. 1974), aggregate percent numbers (%N), percent frequency of occurrence (%FO), and an Index of Relative Importance (IRI, after Pinkas et al. 1971). The IRI (i.e., IRI = %FO(%V + %N) attempts to overcome the shortcomings of using any of these three parameters alone.

RESULTS

COMMON MURRE

Of 31 birds collected, 28 (90%) contained food. The mysid *Neomysis rayii* accounted for 86% of the total IRI, the shrimp *Pandalus borealis* for another 7%, walleye pollock (*Theragra chalcogramma*) for 2% (Table 1). Prey lengths ranged from *Neomysis* mysids of 31 mm to a walleye pollock of 175 mm. Nine *P. borealis* averaged 54 mm and ranged from 52 to 79 mm (front of carapace, less rostrum, to end of urosome), and 162 *Neomysis* averaged 34 mm and ranged from 31 to 44 mm in total length.

Net body weights (whole weight less weight of stomach contents, $n = 31$) ranged from an emaciated specimen of 598 g to 1,228 g and averaged 1,092 g (SD = 130). The weight of stomach contents ranged from zero for three birds to a maximum of 2.9% of the net body weight, and averaged 1% for all specimens. The maximum value was the result of 36 g of food in a bird of 1,224 g.

Murres feed by pursuit diving (Ashmole 1971). The principal prey in this study, mysids and shrimp, occur typically at demersal or epibenthic depths in daylight hours (Mauchline 1980), but the occasional presence of prey such as herring and capelin indicates that the birds probably fed part of the time at mid-depths in the water column. The locations of their collection sites suggest that most birds probably fed over rocky substrates (cf. Science Applications, Inc. 1979) in water depths of about 18 to 55 m.

MARBLED MURRELET

Of 21 birds collected, 20 (95%) contained food and stomach content volume was measured on 18 of these. A minimum of eight species of fish and crustaceans had been eaten, including capelin (61% of IRI), *Thysanoessa* spp. euphausiids (17%), unidentified mysids (9%), and Pacific sand lance (8%, Table 2).

The murrelets' prey ranged in length from euphausiids of 11 mm to sand lance of 135 mm. Mysids (n = 20) averaged 18 mm (SD = 7.4), considerably smaller than those eaten by murres. Measurable capelin (n = 18), the most important prey, averaged 63 mm (SD = 18 mm) and ranged from 28 mm to 105 mm.

Murrelets ($n = 19$) averaged 238 g (SD = 18.8) in net body weight and ranged from 212 g to 280 g. Weights of stomach contents ranged up to 6.6% of net body weight (15 g of food in a bird of 228 g) and averaged 1.8% (SE = 0.42) for all birds sampled. Twelve birds (67%) had values less than 2% and only five birds (28%) had values greater than 5%.

Marbled Murrelets feed by pursuit diving (Ashmole 1971). Water depths where birds were collected were about 4 to 5 m in January and generally ranged between 18 and 45 m thereafter. The murrelets apparently had foraged from mid-depths in the water column to occasionally at or very near the bottom, as attested by the presence of gammarid amphipods and mysids in their diet.

DISCUSSION

There were similarities but also notable differences in the diets of both Marbled Murrelets and Common Murres compared with those reported elsewhere for these species (e.g., Sealy 1975; Ainley and Sanger 1979; Krasnow and Sanger 1986; Fukuyama, Sanger, and Hironaka, unpubl. data). Common Murres eat euphausiids in summer (Scott 1973, Hunt et al. 1981, Schneider and Hunt 1984) and gammarid amphipods in winter (Preble and McAtee 1923). Notwithstanding the fact that one of four murres collected in January 1977 at Kodiak Island had eaten mysids (Krasnow and Sanger 1986), this is the first report of mysids as a dominant food of the species.

Sand lance are generally the most important prey species of Marbled Murrelets throughout most of their range in summer (Carter 1984; Fukuyama et al., unpubl.), although in British Columbia, Pacific herring (*Clupea harengus*) share importance with sand lance in Barkley Sound (Carter 1984), and euphausiids are the staple prey at Langara Island in early summer (Sealy 1975) and at Kodiak in spring (Krasnow and Sanger 1986). Capelin, euphausiids, and particularly mysids were important dietary components of Marbled Murrelets at Kodiak in winter (Krasnow and Sanger 1986). It is clear that Marbled Murrelets are not as generally piscivorous as once believed (Bedard 1969).

The diet of murres in this study varied from winter off California (Baltz and Morejohn 1977), where 24 birds ate mostly fish, some squid, but no crustaceans, and off Newfoundland (Tuck 1960) where 92% of 44 murres had eaten capelin but no crustaceans, and in the North Sea (Blake 1984), where 45% of 403 murres contained fish, 7% had eaten polychaetes, and none had eaten crustaceans. Thus the diet of Common Murres from the present study was unusual not only in it being the first example of their heavy reliance on mysids but in their heavy dependence on crustaceans instead of fish.

The dominance of mysids in the murres' diet further indicated that the birds had foraged at or very near the bottom. Mysids occur throughout the water column at night but migrate to the bottom during daylight hours (Mauchline 1980). This information, along with recent records of Common Murres drowned in fishing gear as deep as 180 m (Forsell and Gould 1981, Piatt and Nettleship 1985) shows that the species can forage near the bottom, although the degree to which they do this

TABLE 2. Winter diet of Marbled Murrelets in Kachemak Bay, Alaska, between January and April 1978. n = 18 stomachs with food; one other bird had an empty stomach and food volume was not measured on two others.

Prey	% Nos. Totals: (n = 654)	% Vol. (82 ml)	% FO[a]	IRI	% Total IRI	Length data (mm) n	$\bar{x}$	SD	Min	Max
Crustaceans										
Unidentified	0.8	1.2	5.6	11	0.2					
Unidentified mysid	34.2	6.7	11.1	456	8.8	20	18	7.4	11	38
Unidentified gammarid amphipod	1.2	1.4	11.1	30	0.6	6	15	2.3	12	18
Euphausiids										
Thysanoessa inermis	0.5	1.2	5.6	9	0.2	2	—	—	15	21
Thysanoessa raschii	19.4	5.7	16.7	418	8.0	38	14	2.3	11	21
Thysanoessa spinifera	0.2	0.9	5.6	6	0.1	1	24	—	—	—
Thysanoessa spp.	22.1	4.0	16.7	435	8.4	24	13	1.6	11	18
Fish										
Unidentified	3.6	8.3	22.2	264	5.1					
Mallotus villosus	11.1	51.8	50.0	3,146	60.6	18	63	18.1	28	105
Unidentified osmerid	0.2	0.1	5.6	1	0.1					
Theragra chalcogramma	0.2	0.2	5.6	2	0.1					
Ammodytes hexapterus	6.4	18.5	16.7	415	8.0	13	45	33.7	29	135

[a] %FO = % frequency of occurrence.

is unknown. Similarly, the occasional presence of mysids and gammarid amphipods in the diet of Marbled Murrelets suggests that this species forages at least part of the time near the bottom. By including detritivores (pandalid shrimp, mysids, and gammarids) in their diets, the murres and murrelets are assured of a broader trophic spectrum than a food supply originating with phytoplankton productivity in the water column alone (cf. Sanger and Jones 1984).

A comparison of prey lengths between the murres and murrelets is noteworthy. Although the average length of all measurable prey from the murres was significantly larger for the murres than for the murrelets (Sanger and Jones 1982), these data are misleading taken at face value. By comparing lengths of the most important prey of the Common Murres (mysids, 86% of IRI, mean length = 34 mm) with those of the Marbled Murrelet (capelin, 61% of IRI, mean length = 63 mm), it is seen that overall the murrelets took as large or larger prey than the murres.

Amounts of food in both species—expressed as percent of net body weight—were generally low. Values ranged from zero in a few specimens to highs of 2.9% for Common Murres and 6.6% for Marbled Murrelets, and averaged 1% and 1.8% for each species, respectively. Although these food weights seem to be low, data on body weight and fat indices (Sanger and Jones 1982) indicated healthy physiological conditions of both species throughout the study.

R. D. Jones, Jr. conducted the field work and was assisted by A. R. DeGange, R. E. Gill, Jr., D. R. Nysewander, M. R. Petersen, and Sanger. D. Wiswar and V. Hironaka processed and identified the stomach contents, and George Mueller and staff at the Marine Sorting Center, University of Alaska, verified their identifications. Earlier drafts of this paper benefitted from reviews by C. J. Lensink, A. R. DeGange, C. H. Halverson, H. Carter, J. Piatt, and two anonymous referees.

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LITERATURE CITED

AINLEY, D. A., AND G. A. SANGER. 1979. Trophic relations of seabirds in the northeastern Pacific Ocean and Bering Sea, p. 95–122. *In* J. C. Bartonek and D. N. Nettleship [eds.], Conservation of marine birds in northern North America. U.S. Fish Wildl. Serv., Wildl. Res. Rep. 11.

ASHMOLE, N. P. 1971. Sea bird ecology and the marine environment, p. 224–286. *In* D. S. Farner and J. R. King [eds.], Avian biology. Vol. 1. Academic Press, New York.

BALTZ, D. M., AND G. V. MOREJOHN. 1977. Food habits and niche overlap of seabirds wintering on Monterey Bay, California. Auk 94:526–543.

BEDARD, J. 1969. Adaptive radiation in Alcidae. Ibis 111:189–198.

BLAKE, B. S. 1984. Diet and fish stock availability as possible factors in the mass death of Auks in the North Sea. J. Exp. Marine Biology and Ecology 76:89–103.

CARTER, H. R. 1984. At-sea biology of the Marbled Murrelet (*Brachyramphus marmoratus*) in Barkley Sound, British Columbia. M.S.thesis, Univ. Manitoba, Winnipeg.

ERIKSON, D. 1977. Distribution, abundance, migration and breeding locations of marine birds in lower Cook Inlet, p. 1–182. *In* L. L. Trasky, L. B.

Flagg, and D. C. Burbank [eds.], Environmental studies of Kachemak Bay and lower Cook Inlet. Vol. 8. Alaska Dept. Fish Game, Anchorage.

FORSELL, D. J., AND P. J. GOULD. 1981. Distribution and abundance of marine birds and mammals wintering in the Kodiak area of Alaska. U.S. Dep. Inter., Fish Wildl. Serv. FWS/OBS-81/13.

FROST, K. J., AND L. F. LOWRY. 1981. Trophic importance of some marine gadids in northern Alaska and their body-otolith size relationships. Fish. Bull. 79:187–192.

HUNT, G. L., JR., B. BURGESON, AND G. A. SANGER. 1981. Feeding ecology of seabirds of the eastern Bering Sea, p. 629–647. *In* D. A. Hood and J. A. Calder [eds.], The eastern Bering Sea shelf: oceanography and resources. Vol. 2. Nat. Ocean. Atmos. Admin., Office of Marine Pollution Assessment. Univ. of Washington Press, Seattle.

KRASNOW, L. D., AND G. A. SANGER. 1986. Feeding ecology of marine birds in the nearshore waters of Kodiak Island, p. 505–630. *In* Environmental assessment of the Alaskan continental shelf. Final reports of principal investigators. Vol. 45. U.S. Dep. Commer., Natl. Ocean. Atmos. Admin. Anchorage, AK.

MARTIN, A. C., R. H. GENSCH, AND C. P. BROWN. 1946. Alternative methods in upland gamebird food analysis. J. Wildl. Manage. 10:8–12.

MAUCHLINE, J. 1980. The biology of mysids and euphausiids. *In* J.H.S. Blaxter, F. S. Russell, and M. Yonge, [eds.], Advances in marine biology. Vol. 18. Academic Press, New York.

MUNRO, J. A., AND W. A. CLEMENS. 1931. Waterfowl in relation to the spawning of herring in British Columbia. Bull. Biol. Bd. Canada, No. 17.

PIATT, J. F., AND D. N. NETTLESHIP. 1985. Diving depths of four alcids. Auk 102:293–297.

PINKAS, L., M. S. OLIPHANT, AND I.L.K. IVERSON. 1971. Food habits of albacore, bluefin tuna and bonito in California waters. Calif. Dep. Fish Game Fish Bull. 152:1–105.

PREBLE, E. A., AND W. L. MCATEE. 1923. A biological survey of the Pribilof Islands, Alaska. Part 1. Birds and mammals. N. Am. Fauna 46:1–128.

SANGER, G. A. 1986. Trophic levels and trophic relationships of seabirds in the Gulf of Alaska, p. 229–257. *In* J. P. Croxall [ed.], Seabird feeding ecology. Cambridge Univ. Press, Cambridge.

SANGER, G. A., AND R. D. JONES, JR. 1982. The winter feeding ecology and trophic relationships of marine birds in Kachemak Bay, Alaska, p. 161–194. *In* Environmental assessment of the Alaskan continental shelf. Final reports of principal investigators. Vol. 16. U.S. Dep. Commer., NOAA. Juneau, AK.

SANGER, G. A., AND R. D. JONES, JR. 1984. Winter feeding ecology and trophic relationships of Oldsquaws and White-winged Scoters on Kachemak Bay, Alaska, p. 20–28. *In* D. N. Nettleship, G. A. Sanger, and P. F. Springer [eds.], Marine birds: their feeding ecology and commercial fisheries relationships. Can. Wildl. Serv. Spec. Publ.

SCHNEIDER, D., AND G. L. HUNT, JR. 1984. A comparison of seabird diets and foraging distribution around the Pribilof Islands, Alaska, p. 86–95. *In* D. N. Nettleship, G. A. Sanger, and P. F. Springer [eds.], Marine birds: their feeding ecology and commercial fisheries relationships. Can. Wildl. Serv., Spec. Publ.

SCIENCE APPLICATIONS, INC. 1979. Lower Cook Inlet interim synthesis report. Bur. Land Mgt./Natl. Ocean. Atmos. Admin., Environ. Assess. Alaskan Cont. Shelf, Boulder, CO.

SCOTT, J. M. 1973. Resource allocation in four sympatric species of marine diving birds. Ph.D.diss., Oregon State Univ., Corvallis.

SEALY, S. G. 1975. Feeding ecology of the ancient and marbled murrelets near Langara Island, British Columbia. Can. J. Zool. 53:418–433.

SHUMACHER, J. D., R. SILLCOX, D. DREVES, AND R. D. MUENCH. 1978. Winter circulation and hydrography over the continental shelf of the northwest Gulf of Alaska. U.S. Dep. Commer., Natl. Ocean. Atmos. Admin. Tech. Rep., ERL 404-PMEL 31: 1–16.

SWANSON, G. A., G. L. KRAPU, J. C. BARTONEK, J. R. SERIE, AND D. H. JOHNSON. 1974. Advantages in mathematically weighting waterfowl food habits data. J. Wildl. Manage. 38:302–307.

TUCK, L. M. 1960. The murres. Canadian Wildlife Series: 1. Ottawa.