OVERLAP IN DIETS AND FORAGING OF COMMON MURRES (*URIA AALGE*) AND RHINOCEROS AUKLETS (*CERORHINCA MONOCERATA*) AFTER THE BREEDING SEASON

Monique M. Lance[1,3] and Christopher W. Thompson[2,4]

[1]*Washington Department of Fish and Wildlife, 7801 Phillips Road S.W., Tacoma, Washington 98498, USA; and*
[2]*Washington Department of Fish and Wildlife, 16018 Mill Creek Boulevard, Mill Creek, Washington 98012, USA*

Abstract.—Common Murres (*Uria aalge*; hereafter "murres") and Rhinoceros Auklets (*Cerorhinca monocerata*; hereafter "auklets") breed and forage sympatrically over much of their range. They have similar diets during the breeding season, which suggests that they partition prey during the breeding season by foraging (1) at different locations, (2) at different times of day, (3) at different water depths, (4) on different proportions of the same prey species, or (5) some combination of the four. We examined possible mechanisms of niche partitioning during late summer and fall in Puget Sound, Washington, in 1993–1996. Murres and auklets fed mainly on Pacific herring (*Clupea pallasii*, occurring in 74.2% and 48.1%, respectively, of gastrointestinal tracts with contents), Pacific sand lance (*Ammodytes hexapterus*; 45.8% and 62.3%), and salmonid (*Oncorhynchus* spp.) species (21.9% and 9.7%). Auklets also consumed considerable amounts of threespine stickleback (*Gasterosteus aculeatus*; 26.6%). Murres and auklets did not differ significantly (1) in their diet (between age classes or sexes of either species, or among years); (2) in mean lengths of Pacific herring (101 and 109 mm, respectively) and Pacific sand lance (82 and 86 mm) they consumed; or (3) in the mean depth (7–8 m) at which they were entangled in gill nets. Dietary diversity was low, with most gastrointestinal tracts containing only one or two prey species in both murres and auklets. Murres were caught and therefore presumably feed more frequently in the afternoon and evening; whereas auklets were entangled more often in early morning. We found differences between murres and auklets in the diel chronology of prey taken, which may partly explain how murres and auklets coexist during the breeding season and months thereafter, prior to auklet emigration from Puget Sound. *Received 23 January 2003, accepted 18 January 2005.*

Key words: alcid, *Cerorhinca monocerata*, Common Murre, foraging ecology, niche partitioning, Rhinoceros Auklet, *Uria aalge*, Washington.

Chevauchement du Régime Alimentaire et de la Quête Alimentaire chez *Uria aalge* et *Cerorhinca monocerata* après la Saison de Reproduction

Résumé.—*Uria aalge* et *Cerorhinca monocerata* nichent et recherchent leur nourriture en sympatrie. Ils ont des régimes alimentaires similaires au cours de la période de reproduction, ce qui suggère qu'ils se divisent les proies au cours de cette période en effectuant leurs recherches (1) à des endroits différents, (2) à des moments différents de la journée, (3) à différentes profondeurs d'eau, (4) en prélevant des proportions différentes pour une même espèce de proie, ou (5) une combinaison des quatre. Nous avons examiné les mécanismes possibles de la division de niches, à la fin de

[3]E-mail: lancemml@dfw.wa.gov
[4]Present address: School of Aquatic and Fishery Sciences, Box 355020, University of Washington, Seattle, Washington 98195, USA.

l'été et au cours de l'automne, à Puget Sound, Washington, en 1993-1996. *Uria aalge* et *Cerorhinca monocerata* se nourrissaient principalement de *Clupea pallasii* (représentant 74,2% et 48,1%, respectivement, du contenu gastrointestinal), *Ammodytes hexapterus* (45,8% et 62,3%) et *Oncorhynchus* spp. (21,9% et 9,7%). *Cerorhinca monocerata* ont consommé des quantités considérables de *Gasterosteus aculeatus* (26,6%). *Uria aalge* et *Cerorhinca monocerata* ne différaient pas de manière significative (1) dans leur régime alimentaire (entre les classes d'âge ou les sexes quelque soit l'espèce, ou parmi les années), (2) dans la longueur moyenne de *Clupea pallasii* (101 et 109 mm, respectivement) et *Ammodytes hexapterus* (82 et 86 mm) qui ont été consommés, ou (3) dans la profondeur moyenne (7-8 m) à laquelle ils ont été capturés grâce à des filets à mailles. La diversité du régime alimentaire était faible, avec un contenu gastrointestinal constitué d'une ou deux espèces de proie seulement chez les deux espèces étudiées. *Uria aalge* a été attrapé plus fréquemment au cours de l'après-midi et de la soirée, traduisant probalement le fait que cette espèce se nourrit davantage au cours des ces périodes de la journée. Par contre, *Cerorhinca monocerata* a été capturé, plus souvent, tôt le matin. Nous avons trouvé des différences entre ces deux espèces dans la chronologie journalière des proies capturées. Ceci pourrait en partie expliquer comment *Uria aalge* et *Cerorhinca monocerata* coexistent au cours de la saison de reproduction et les mois qui suivent, avant l'émigration de *Cerorhinca monocerata* de Puget Sound.

Along the west coast of North America, Common Murres (*Uria aalge*, hereafter "murres") and Rhinoceros Auklets (*Cerorhinca monocerata*, hereafter "auklets") have widely overlapping breeding ranges. During the breeding season, they also have similar diets at breeding colonies and at sea in Washington and British Columbia (Richardson 1961, Sealy 1973, Leschner 1976, Wilson and Manuwal 1986, Vermeer 1993, Bertram and Kaiser 1993). Murres and auklets may reduce competition between themselves by foraging (1) at the same prey patches, but at different water depths; (2) at different prey patches (e.g. that differ in density); (3) at different times of day or night (Piatt 1990); or (4) some combination of the three. However, these species have different migratory patterns and wintering ranges. Specifically, in late summer and fall, tens of thousands of murres typically immigrate to the Strait of Juan de Fuca, Strait of Georgia, and Puget Sound; whereas most auklets emigrate from those areas to the outer coast of British Columbia, Washington, Oregon, and California (Manuwal et al. 1979, Vermeer 1983, Mahaffy et al. 1994). That suggests that murres and auklets may adopt different strategies for partitioning prey resources during the nonbreeding season than they use during the breeding season.

The late summer diet, but not the fall or winter diet, of adult murres has been studied in those areas of the Pacific Northwest (Vermeer 1983, 1993). Similarly, no published studies exist regarding the nonbreeding diet of auklets. Thus, the purpose here was to document the diets of murres and auklets during the nonbreeding season in the same general location (Puget Sound, Washington) and period (late summer and fall) to assess how differences in prey composition, prey size, foraging depth, diel patterns of foraging, or all four, contribute to niche partitioning between these species during the nonbreeding season as compared with the breeding season. Our specific objectives were to document (1) prey species consumed and their mean lengths; (2) variation in diet in relation to age and sex of murres and auklets, season (summer vs. early fall) and year; (3) diet diversity; and (4) diet composition in relation to time of day and water depth at which birds were entangled in gill nets.

Materials and Methods

Specimen collection.—Murres and auklets were incidentally entangled in Puget Sound, Washington, in drift gill nets set for sockeye (*Oncorhynchus nerka*) and chum (*O. keta*) salmon during summer and fall in 1993 and 1994; in test fisheries for sockeye and chum in 1995 (Melvin and Conquest 1996); and in test fisheries for sockeye in 1996 (Fig. 1; Melvin et al. 1997).
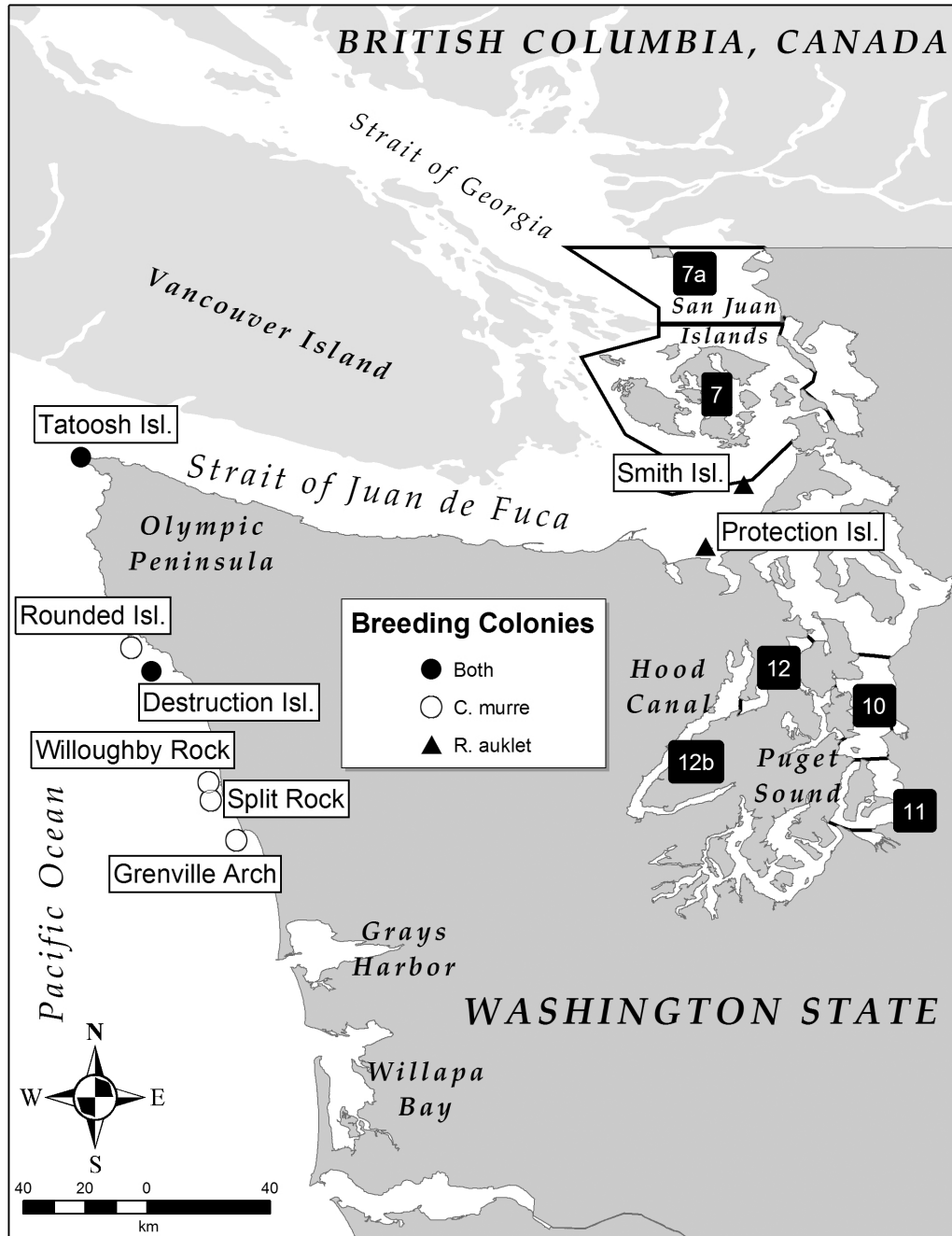
Fig. 1. Map of the study area indicating (1) summer sockeye salmon fishing areas (7 and 7a) in northern Puget Sound; (2) fall chum salmon fishing areas (10, 11, 12, and 12b) in Hood Canal and central Puget Sound, Washington; and (3) Common Murre and Rhinoceros Auklet breeding colonies in Washington.

Collection dates during the sockeye season in fishing areas 7 and 7a (Fig. 1) were 1–30 August 1993, 3–22 August 1994, 29 July–23 August 1995, and 28 July–28 August 1996. Collection dates during the chum salmon season in fishing areas 10/11, 12, and 12b (Fig. 1) were 2 September–8 November 1993, 7 September–8 November 1994, and 25 October–11 November 1995. Seabirds were collected from Washington Department of Fish and Wildlife (WDFW) gill-net test fisheries in 1993 from 6 July through 1 August. "Summer" and "fall" are used to describe the sockeye and chum gill net seasons, respectively.

During the sockeye and chum fishery season in 1993, seabirds were collected from nontreaty and treaty fisheries, resulting in fishing essentially 24 h per day (S. Boessow pers. comm.). In 1994, sockeye fishery openings were typically between 1900 and 0700 hours, and chum fishery openings typically between 1600 and 0800 hours. In the 1995 sockeye season, experimental nets were fished over 24-h periods whereas during the 1995 chum and 1996 sockeye seasons, fishing was restricted to 1.5 h before sunrise to 1.5 h after sunset; boats did not fish at night (Melvin et al. 1999, Melvin and Parrish 2001).

In general, drift gill nets were 25 m deep and 549 m long for sockeye salmon, and 23 m deep and 549 m long for chum salmon. Test fisheries in 1995 and 1996 used experimental nets (Melvin and Conquest 1996, Melvin et al. 1997). Dead entangled birds were placed on ice after collection to halt digestive processes and either necropsied fresh or frozen immediately.

Data collection.—Data collected from each bird included body mass (g), exposed culmen length (mm), plumage type (hatch-year vs. older), presence or absence of flight-feather molt, sex, reproductive condition, presence or absence of a brood patch, and condition of bursa of Fabricius. To assess sex and reproductive condition, (1) ovary and testes length and width were recorded to the nearest millimeter; (2) ovary condition was described as granular and nondifferentiated, or follicles were measured to the nearest millimeter; and (3) dilation of the oviduct was noted. Bursa of Fabricius condition was described as large and fleshy, thin-walled, or membranous (absent).

Murres and auklets were assigned to two age categories: subadult and adult. Birds with fleshy bursae (Broughton 1994), no indication of reproductive organ maturity (e.g. tiny,

relatively undifferentiated gonads and associated reproductive structures, such as oviducts), in juvenal or first basic plumage (or first prebasic molt between those plumages and lacking flight-feather molt) were considered subadult birds. Those birds are believed to be mainly hatching-year juveniles (hatched during the current calendar year), but because the sample may contain some subadults (hatched at least one calendar year earlier, but not yet reproductive) that match the criteria above, the category was conservatively labeled "subadults." Birds with thin-walled or membranous bursae and mature reproductive systems (e.g. large ovarian follicles, hypertrophied oviducts, or both) and in breeding (alternate) plumage or adult (definitive) basic plumage, with a brood patch (Baker 1993), or with flight feather molt were considered adults. Culmen length and body mass were useful indicators of age in some instances.

Whole fish were measured from the tip of the snout to the fork in the tail, and cephalopods were measured from the tip of the mantle to the end of the longest tentacle. Because dietary data collected using gill nets as sampling devices may be biased in various ways (Ogi and Tsujita 1973, Bradstreet 1980, Gaston and Noble 1985), the entire gastrointestinal tract was divided, and prey found in the esophagus and proventriculus indicating recent consumption were kept separate from those in the ventriculus and intestines, for time-of-day and depth analyses only. Items believed to be present because of secondary ingestion (secondary prey observed leaking from primary prey) were deleted. Hard parts were cleaned (flesh removed) and stored dry; cephalopod beaks were stored in isopropyl alcohol.

Prey were identified to the lowest possible taxon, using a dissecting microscope, a reference bone collection of fishes collected from Washington and Oregon, and published bone and otolith keys (Morrow 1979, Cannon 1987). A random subsample (10–15%) from 1993 and 1994 was sent to Pacific Identifications (University of Victoria, Anthropology Department) for independent and blind verification.

Statistical analyses.—Data were analyzed using SYSTAT 5.0 (Wilkinson 1992). Percentage data were arcsine square-root transformed (Sokal and Rohlf 1995). Time-of-day and water-depth analyses were confined to prey collected from esophagi and proventriculi. In

multiple comparison analyses, the Dunn-Šidák correction was used (Sokal and Rohlf 1995), and alpha (α) was set at variable levels accordingly. Analyses of dietary diversity were based on the number of different prey species present in a gastrointestinal tract. For time-of-day analyses, times (Pacific Standard Time, PST) were grouped hourly starting at midnight. Analyses of time of day in relation to consumption of specific prey species were done using two-way and three-way contingency tables for within- and between-species comparisons, respectively. The depths at which birds were entangled in gill nets (1996 sockeye fishery only) were recorded in meshes (1 mesh = 127 mm).

Results

Diet composition.—Data analyses are based on the 68.2% of murre (*n* = 522) and 84.2% of auklet (*n* = 183) gastrointestinal tracts that contained identifiable prey. Murres and auklets fed primarily on Pacific herring (74.2% and 48.1% occurrence, respectively, in gastrointestinal tracts with prey), Pacific sand lance (45.8% and 62.3%), and salmon (21.9% and 9.8%) but in somewhat different proportions (Table 1). Auklets also ate many threespine stickleback (26.6% occurrence), whereas murres did not (1.7%; Table 2). Scientific names for marine species are given in Tables 1 and 2.

Prey lengths.—Prey ranged in mean length from 27 to 175 mm for murres and 26 to 109 mm for auklets (Table 3). Mean length of herring (*t* = 0.965, df = 15, *P* = 0.352) and sand lance (*t* = 1.083, df = 67, *P* = 0.295) preyed on by murres and auklets were not significantly different (Table 3). Similar analyses for other fish species were not possible because of inadequate sample sizes.

Age and sex.—There was no significant effect of bird age (subadult vs. adult) or sex on the relative frequency of herring, sand lance, or salmon found in murres (experimentwise α = 0.017; age: *F* ≤ 7.722, df = 1 and 24, *P* ≥ 0.017; sex: *F* ≤ 1.672, df = 1 and 24, *P* ≥ 0.232) or auklets (age: *F* ≤ 6.046, df = 1 and 24, *P* ≥ 0.039; sex: *F* ≤ 1.000, df = 1 and 24, *P* ≥ 0.347) during summer and fall.

Year and season.—Percentage of herring, sand lance, and salmon in the diets of murres and auklets differed between seasons in some cases, but not within seasons among years (experimentwise α = 0.017; herring: ANOVA, *F* ≤ 2.992, df = 2 and 18, *P* ≥ 0.076; sand lance: *F* ≤ 2.132, df = 2 and 18, *P* ≥ 0.148; salmon: *F* ≤ 2.132, df = 2 and 18, *P* ≥ 0.148; Table 1). Therefore, within seasons, data for all years were combined.

Among years, no differences in diet were found between seasons in murres or auklets, except that murres fed more frequently on sand lance (*F* = 13.616, df = 1 and 18, *P* = 0.002) and salmon (*F* = 9.512, df = 1 and 18, *P* = 0.006) in summer than in fall (Table 1). Similarly, no differences in diet were found within seasons between murres or auklets, except that herring and salmon occurred more frequently in summer in the diet of murres than in the diet of auklets (herring: *t* = 3.871, df = 30, *P* = 0.001; salmon: *t* = 0.109, df = 30, *P* = 0.005; Table 1).

Dietary diversity.—Most murre and auklet gastrointestinal tracts contained one (49% and 42%, respectively, all years combined) or two (31% for both) prey species, but rarely contained as many as five or six prey species (Table 4). Dietary diversity did not differ within or between seasons, years, or species, except that it was significantly lower in murres in 1993 than in 1996 (Kolmogorov-Smirnov Test, *D* = 0.456, *P* < 0.001; Table 4) and was greater in auklets than in murres in fall 1995 (*D* = 0.778, *P* = 0.005) and summer 1996 (*D* = 0.298, *P* < 0.001; Table 4).

TABLE 1. Percentage occurrence of Pacific herring, Pacific sand lance, and salmon species in gastrointestinal tracts of Common Murres and Rhinoceros Auklets caught in gill nets in sockeye and chum fisheries in Puget Sound, Washington (1993–1996 combined).

	Common Murre		Rhinoceros Auklet	
Prey species	Sockeye	Chum	Sockeye	Chum
Pacific herring (*Clupea pallasii*)	72.5	86.0	42.0	94.4
Pacific sand lance (*Ammodytes hexapterus*)	50.5	11.6	67.6	22.2
Salmon (*Oncorhynchus* spp.)	24.0	7.0	9.6	11.1
Number of birds	313	43	136	18

Table 2. Percentage of occurrence of prey species other than Pacific herring, Pacific sand lance, and salmon found in gastrointestinal tracts of Common Murres ($n = 356$) and Rhinoceros Auklets ($n = 154$) caught in gill nets in Puget Sound, Washington (fisheries and years combined).

Prey species	Common Murres		Rhinoceros Auklets	
	%	(n)	%	(n)
Pacific tomcod (*Microgadus proximus*)	11.8	(48)	10.4	(16)
Pacific hake (*Merluccius productus*)	6.5	(23)	0.0	(0)
Squid spp.	5.9	(21)	11.0	(17)
Pacific sandfish (*Trichodon trichodon*)	3.4	(12)	5.2	(8)
Shiner surfperch (*Cymatogaster aggregata*)	2.5	(9)	1.9	(3)
River lamprey (*Lampetra ayresi*)	2.2	(8)	3.9	(6)
Threespine stickleback (*Gasterosteus aculeatus aculeatus*)	1.7	(6)	26.6	(41)
Rockfish (*Sebastes* spp.)	1.4	(5)	0.0	(0)
Juvenile crab (infraorder Brachyura)	0.8	(3)	7.8	(12)
Polychaete (class Polychaeta)	0.8	(3)	1.9	(3)
Plainfish midshipman (*Porichthys notatus*)	0.6	(2)	0.6	(1)
Bay pipefish (*Syngnathus leptorhynchus*)	0.3	(1)	3.9	(6)
Surf smelt (*Hypomesus pretiosus*)	0.3	(1)	0.6	(1)
Tube-snout (*Aulorhynchus flavidus*)	0.3	(1)	0.6	(1)
Miscellaneous invertebrate species	0.9 [a]	(4)	4.5 [b]	(5)
Unidentified fish	0.8	(3)	0.0	(0)

[a] Amphipod or shrimp and unidentified invertebrate ($n = 2$), Purple Sea Urchin (*Strongylocentrotus purpuratus*; $n = 1$), bumble bee ($n = 1$).

[b] Amphipod or shrimp and unidentified invertebrate ($n = 5$).

Table 3. Length (mm) of major whole-prey items found in the gastrointestinal tracts of Common Murres and Rhinoceros Auklets caught in gill nets in Puget Sound in 1993–1996.

Prey species	Common Murre prey			Rhinoceros Auklet prey		
	n	Mean ± SE	Range	n	Mean ± SE	Range
Pacific herring	15	100.8 ± 7.3	73–195	2	108.5 ± 3.5	105–112
Pacific sand lance	55	81.8 ± 1.2	60–102	14	86.2 ± 3.9	72–122
Oncorhynchus spp.	3	122.9 ± 13.8	100–148	0	–	–
Threespine stickleback	0	–	–	60	25.7 ± 0.8	18–53
Bay pipefish	2	27.0 ± 2.0	25–29	7	61.6 ± 10.3	40–114
Squid spp.	3	175.0 ± 13.2	150–195	0	–	–
River lamprey	2	143.5 ± 1.5	142–145	0	–	–

Time of day.—Murres were caught more frequently in the afternoon and evening, whereas auklets were entangled more often in early morning ($\chi^2 = 25.95$, df = 5, $P < 0.001$; Fig. 2). Murres preyed on herring more frequently than sand lance in the evening (1800–2400 hours) and on sand lance more frequently than herring in the morning and early afternoon (0600–1500 hours) ($\chi^2 = 10.14$, df = 2, $P = 0.006$; Fig. 3A). By contrast, auklets fed equally on herring and sand lance at all times of day ($\chi^2 = 4.60$, df = 2, $P = 0.10$; Fig. 3B). Murres and auklets did not differ in timing of their consumption of herring (Mantel-Haenszel $\chi^2 = 0.895$, $P = 0.344$); however, sand lance occurred more frequently throughout the day in auklets than in murres (Mantel-Haenszel $\chi^2 = 20.737$, $P < 0.001$; Fig. 3A, B).

Water depth.—Most murres and auklets were entangled in nets at similar water depths, usually <10 m deep ($D = 0.065$, $P = 0.956$; Fig. 4).

Murre and Rhinoceros Auklet Diet

TABLE 4. Percentage of Common Murre (CM) and Rhinoceros Auklet (RA) gastrointestinal (GI) tracts containing between one and six different prey species by year and fishery; sample sizes in parentheses.

Number of prey in GI tract	Sockeye fishery								Chum fishery	
	1993		1994		1995		1996		1993–1995 [a]	
	CM (51)	RA (9)	CM (67)	RA (37)	CM (8)	RA (13)	CM (187)	RA (77)	CM (43)	RA (18)
1	62.8	44.4	46.3	35.1	37.5	15.4	42.8	50.7	67.4	33.3
2	25.5	33.3	32.8	46.0	37.5	53.9	32.1	16.9	30.2	44.4
3	7.8	22.2	11.9	13.5	12.5	7.7	14.4	19.5	2.3	16.7
4	2.0	0.0	9.0	2.7	12.5	23.1	6.4	10.4	0.0	5.6
5	0.0	0.0	0.1	2.7	1.6	0.0	0.0	2.6	0.0	0.0
6	2.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0

[a] Years combined because median prey diversity did not differ significantly among years.
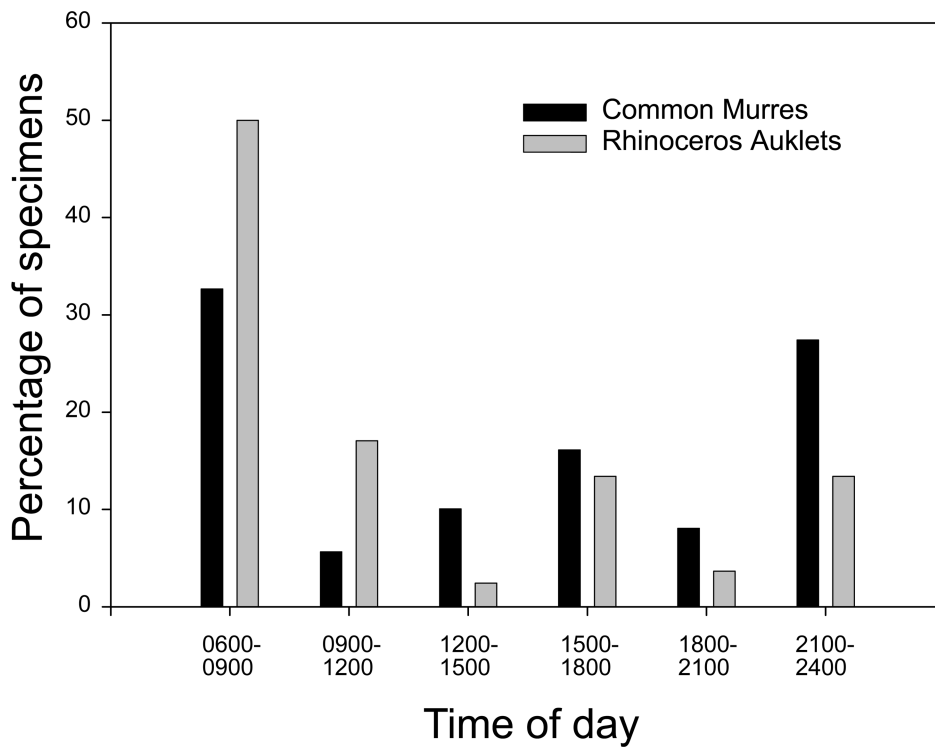

FIG. 2. Frequency of entanglement (%) of Common Murres (*n* = 248) and Rhinoceros Auklets (*n* = 82) in relation to time of day in gill nets in the 1996 sockeye fishery (28 July to 28 August) in Puget Sound, Washington.

DISCUSSION

Diet composition.—Murres and auklets in northern Puget Sound fed mainly on herring, sand lance, salmon, and stickleback in summer and fall of 1993–1996. Most other studies also showed that in the summer in nearshore habitats, both species feed primarily on small schooling fish that are long and narrow in girth, such as anchovy (*Engraulis mordax*), capelin
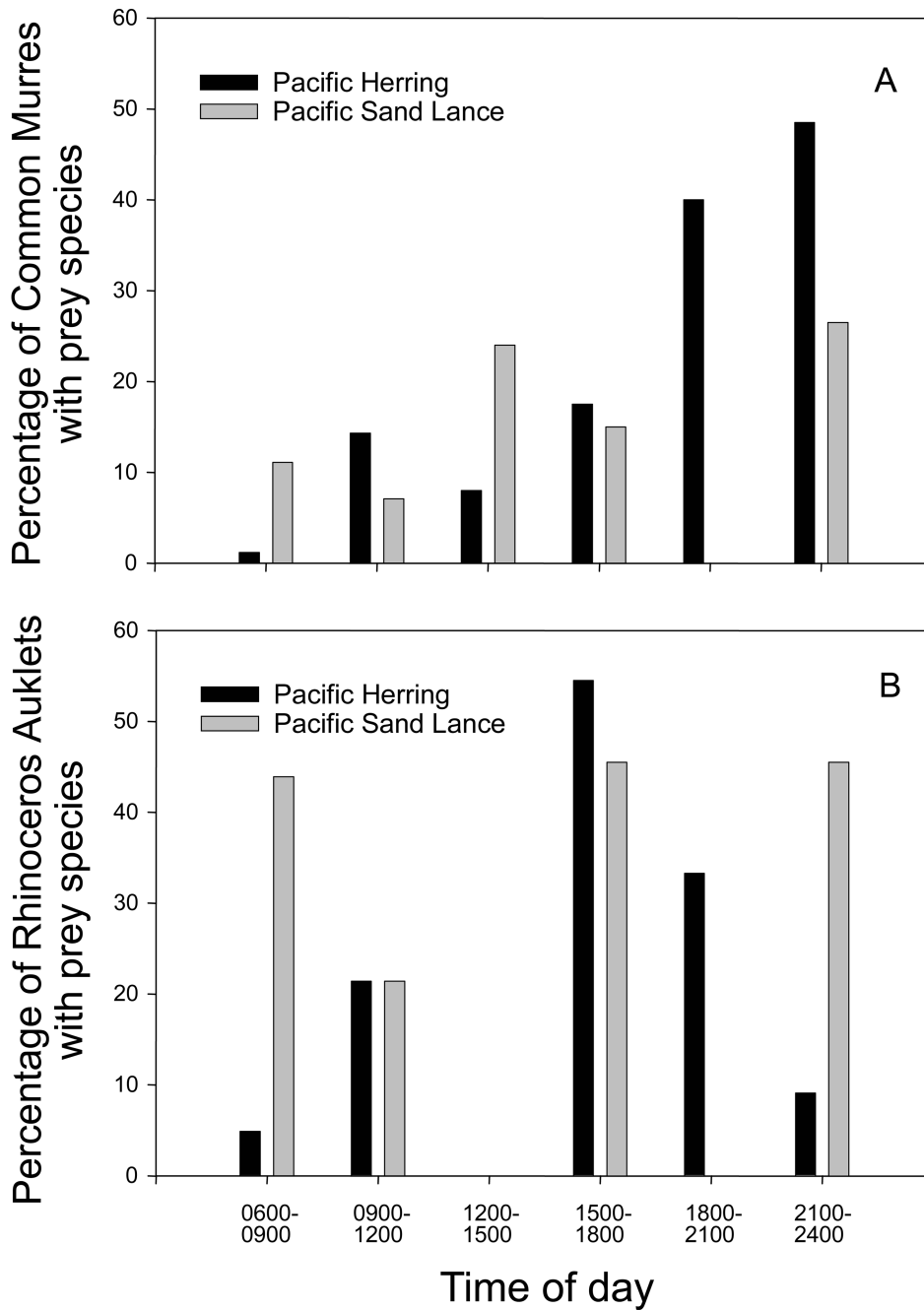
FIG. 3. Frequency of occurrence (%) in each period of the day (e.g. 0600–0900 hours) of Pacific herring and Pacific sand lance in the esophagi and proventriculi of (A) Common Murres (n = 186) and (B) Rhinoceros Auklets (n = 46) entangled in gill nets in the sockeye salmon fishery in Puget sound, Washington in 1996.

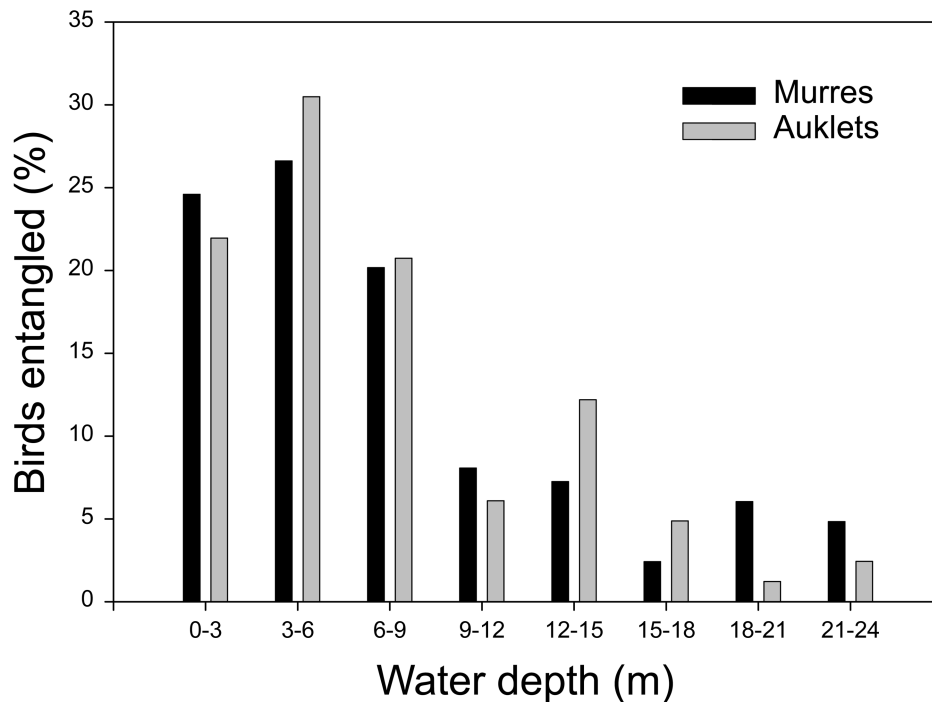Fig. 4. Water depth at which Common Murres (*n* = 248) and Rhinoceros Auklets (*n* = 82) were entangled in gill nets in the sockeye fishery in Puget Sound, Washington, in summer 1996. Nets did not exceed 25 m in depth.

(*Mallotus villosus*), and sand lance (Ainley and Sanger 1979, Bradstreet and Brown 1985, Ainley et al. 2002). The predominance of herring, sand lance, salmon, and stickleback in murre and auklet diets coincides with high concentrations of juveniles of those prey species in Puget Sound at that time of year, and likely indicates that both murres and auklets forage opportunistically on prey that is locally abundant (Hart 1973, Wootton 1976, Fresh 1979, Matthews 1983, Croll 1990, Burger et al. 1993, Penttila 1995). That auklets foraged regularly on shallow-living stickleback (Wootton 1976), whereas murres rarely did so, probably reflects the smaller bill size and reduced diving ability of auklets as compared with murres (Bédard 1985, Burger et al. 1993). Four other prey species occurred frequently in the diets of murres and auklets: tomcod, hake, squid, and sandfish; however, those species probably were over-represented because of longer mean residence times of their hard parts (Hilton et al. 1998, 2000), especially squid beaks (Bradstreet 1980, Gaston and Noble 1985); conversely, readily digestible invertebrates that contained no hard parts may have been underestimated in the diet (Hilton et al. 1998, 2000).

Between-species comparisons.—The most significant difference in diet between murres and auklets was that murres ate more of the two largest prey species, herring and salmon; whereas auklets ate more of the two smaller prey species, sand lance and stickleback. Because alcids swallow their prey whole, body size and bill morphology dictate optimal as well as maximum prey length and, more importantly, prey girth or cross-sectional area (Swennen and Duiven 1977). In turn, because adult auklets (550 g) weigh only ~55% as much as murres (990 g; Gaston and Dechesne 1996, Thompson et al. 1998, Ainley et al. 2002), one would expect that auklets would consume smaller prey, on average, than murres. That is corroborated by captive studies in which Razorbills (*Alca torda*), similar in body size (~580 g) to auklets, preferred herring that were only about one-half the size of those preferred by murres (Swennen and Duiven 1977). Thus, quantitative

and qualitative differences in prey composition between murres and auklets are attributable, at least partly, to differences in mean length and girth of various prey species (Table 3).

Prey lengths.—Murres and auklets did not differ in the mean lengths of herring (109 and 101 mm, respectively) and sand lance (86 and 82 mm) they consumed. In other studies, murres and auklets also consumed similar sizes of herring and sand lance (Burger et al. 1993, Gaston and Dechesne 1996, Ainley et al. 2002), indicating that these birds consumed mainly first-year (i.e. 0-age class), but occasionally second-year fish (Fresh 1979, Dick and Warner 1982, Field 1988, Grosse and Hay 1988).

Age and sex.—Murre chicks fledge at 20–24 days of age when they are ~20% of adult mass and incapable of flight. Chicks are accompanied by their male parent at sea; the male guards and leads them to major foraging areas and provides food for 1–2 months (Ainley et al. 2002). Because adult males are feeding chicks, it is reasonable to expect no differences in diet composition between chicks and adult males during that time. Because female parents do not accompany their chicks at sea and are free to forage over a broader area with potentially different prey, one might expect differences in diet between adult males and females during the postfledging period (Harris and Birkhead 1985, Gaston and Dechesne 1996, Hatch et al. 2000); however, we found no dietary differences between ages or sexes. Similarly, diet composition did not differ between adult and subadult Thick-billed Murres (*U. lomvia*) studied in the eastern Canadian Arctic (Gaston and Bradstreet 1993) or between adult male and female murres in the North Sea off Scotland (Halley et al. 1995), but Scott (1990) found that murre chicks fed on slightly different prey types (anchovies) than their accompanying male parent.

In contrast to murres, auklets fledge at ~50 days of age, when they are about 75% to 85% of adult size and mass, volant, and independent of their parents (Gaston and Dechesne 1996). Adult females average slightly smaller (456 g) than males (510 g), but there is broad overlap (Gaston and Dechesne 1996). We found no difference in diet between auklet ages or sexes. Differences in diet during the breeding season between adults and chicks have been described (Vermeer et al. 1987, Davoren and Burger 1999), but we are not aware of any studies that have compared diets between ages or sexes of auklets after the breeding season.

Year and season.—The relative frequency of herring, sand lance, and salmon in murres or auklets did not vary significantly among years within each fishery. Although some other multi-year studies of food habits in murres (Ainley et al. 1990) and auklets (Wilson and Manual 1986) have shown little interannual variation in diet during the breeding season, many have shown large variability in both the species consumed and their relative proportions within and outside the breeding season (Gaston and Dechesne 1996, Ainley et al. 2002).

Murres ate more sand lance and salmon in summer than in fall. By contrast, auklets showed no differences in diet between seasons, but that may be the result of a small fall sample. Within seasons, murres and auklets did not differ in diet, except that murres consumed a greater proportion of herring and salmon in summer than auklets. Those results are consistent with the notion that murres and auklets opportunistically exploit prey that are available throughout Puget Sound in both seasons, but whose abundances and distributions fluctuate seasonally and spatially within Puget Sound.

Dietary diversity.—Most murre and auklet gastrointestinal tracts contained only one or two prey species, usually herring or sand lance. Herring, sand lance, and stickleback are all species that form schools (Wootton 1976, Field 1988, Grosse and Hay 1988). Schools are usually composed of a single species; however, juvenile herring and sand lance may form mixed aggregations when feeding near the surface (Hobson 1986). The predominance of gastrointestinal tracts with one and two species may result from feeding at single- or two-species schools, or pursuing only single species of prey in multi-species schools of fish (Sanford and Harris 1967). Gastrointestinal tracts that contain many prey species may reflect prolonged residence times of hard parts of some species (discussed above). Prey species diversity among murres off the Oregon coast was similar, with most individuals having one, two, or three prey species in their gastrointestinal tracts (Matthews 1983).

Time of day.—The only significant relationship between diet and time of day in murres or auklets was that murres preyed on herring more frequently than on sand lance in the evening (1800–2400 hours) and on sand lance more

frequently than on herring in the morning and early afternoon (0600–1500 hours). That is probably because sand lance form schools during the day and bury themselves in sandy substrates at night and thus are not available (Field 1988, Robards et al. 1999), whereas juvenile herring typically form tight schools, or "bait balls," when feeding near the surface at dawn and dusk (1–6 m) and spread out more evenly in the shallow water column (3–15 m) during the day and at night (Hourston 1959).

Most other studies found that murres fed most intensively at dawn and dusk, less during midday, and not at all at night (Sanford and Harris 1967, Ogi and Tsujita 1973, Burger and Piatt 1990), though Melvin et al. (1997) documented nocturnal feeding, as did Croll et al. (1992) in Thick-billed Murres. Previous studies of daily patterns of foraging behavior of auklets during the breeding season found that adult auklets fed mainly during the day and at dusk, but sometimes at night (Grover and Olla 1983, Vermeer et al. 1987, Wahl and Speich 1994, Gaston and Dechesne 1996), which largely agrees with our results.

Water depth.—Although gill nets in which murres and auklets were captured were 23–25 m deep, murres and auklets were entangled at mean depths of 7.8 and 7.1 m, respectively. At the peak foraging times of murres and auklets, their primary prey, herring and sand lance, tend to occur within 10 m of the surface (Hourston 1959, Girsa and Danilov 1976, Fresh 1979, Hobson 1986, Field 1988, Grosse and Hay 1988). That may explain why those birds were mainly entangled at relatively shallow depths. In addition, the mean depths at which murres and auklets were entangled are consistent with time-depth recorder studies that found that auklets in British Columbia spent 90% of their underwater foraging at depths <10 m (Burger et al. 1993). Similarly, dives by Thick-billed Murres in the Northwest Territories were generally <20 m (Croll et al. 1992). Thus, although auklets and murres can dive as deep as 60 and 180 m, respectively (Burger and Simpson 1986, Burger et al. 1993), and that difference in diving ability may explain differences in diet at other locations, times of year, or both, differences in diving ability do not appear to be correlated with dietary differences observed here, because we found no difference in the mean depths at which murres and auklets were entangled.

Seasonal niche separation between murres and auklets.—Sympatric and ecologically similar seabirds may coexist by reducing competition between themselves by foraging (1) at the same prey patches, but at different water depths; (2) at different prey patches (e.g. that differ in density); (3) at different times of day or night; or (4) some combination of the three. For example, Piatt (1990) examined responses of murres and Atlantic Puffins (*Fratercula arctica*) to schools of capelin and observed species differences in response to capelin density and depth. Murres were observed foraging on denser schools of capelin deeper within the water column than puffins, which concentrated on smaller schools occurring higher in the water column. Piatt (1990) suggested that the larger body size and associated higher food demand of murres explained those observed differences.

Here, murres were caught more frequently in the afternoon and evening, whereas auklets were entangled more often in early morning. In addition, murres preyed on herring more frequently than on sand lance in the evening and on sand lance more frequently than on herring in the morning and early afternoon, probably because of diel movements of sand lance in the water column. Those differences in foraging may partly explain how murres and auklets coexist during the breeding season and months thereafter, before auklet emigration from Puget Sound.

Prey abundance and distribution during the nonbreeding season can strongly influence adult and subadult survival (Nur and Sydeman 1999), and can be the primary factor driving seasonal and interannual changes in seabird distribution and abundance. Thus, the most likely reason that seabirds immigrate into an area, such as Puget Sound, for the duration of the nonbreeding season is to exploit abundant and predictable prey resources in the area. Coexistence of ecologically similar species can be mediated by partitioning limiting resources in time, space, or both (e.g. foraging at different times of day, locations, or water depths, or on different sizes or species of prey). However, we observed only minor differences in foraging behavior between auklets and murres in late summer and fall, when the two species coexist, and just before departure of most auklets from Puget Sound. Therefore, it is likely that studies of murre and auklet diets in winter in the Pacific

Northwest would help indicate the mechanisms by which murres and auklets partition their environment in areas of sympatry.

Acknowledgments

Literature Cited

Ainley, D. G., D. N. Nettleship, H. R. Carter, and A. E. Storey. 2002. Common Murre (*Uria aalge*). *In* The Birds of North America, no. 666 (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.

Ainley, D. G., and G. A. Sanger. 1979. Trophic relations of seabirds in the northeastern Pacific Ocean and Bering Sea. Pages 95–122 *in* Conservation of Marine Birds of Northern North America (J. C. Bartonek and D. N. Nettleship, Eds.). U.S. Fish and Wildlife Service, Wildlife Research Report, no. 11.

Ainley, D. G., C. S. Strong, T. M. Penniman, and R. J. Boekelheide. 1990. The feeding ecology of Farallon seabirds. Pages 51–127 *in* Seabirds of the Farallon Islands: Ecology, Dynamics, and Structure of an Upwelling-system Community (D. G. Ainley and R. J. Boekelheide, Eds.). Stanford University Press, Stanford, California.

Baker, K. 1993. Identification Guide to European Non-passerines. British Trust for Ornithology, Thetford, United Kingdom.

Bédard, J. 1985. Evolution and characteristics of the Atlantic Alcidae. Pages 1–51 *in* The Atlantic Alcidae: The Evolution, Distribution and Biology of the Auks Inhabiting the Atlantic Ocean and Adjacent Water Areas (D. N. Nettleship and T. R. Birkhead, Eds.). Academic Press, New York.

Bertram, D. F., and G. W. Kaiser. 1993. Rhinoceros Auklet (*Cerorhinca monocerata*) nestling diet may gauge Pacific sand lance (*Ammodytes hexapterus*) recruitment. Canadian Journal of Fishery and Aquatic Science 50:1908–1915.

Bradstreet, M. S. W. 1980. Thick-billed Murres and Black Guillemots in the Barrow Strait area, N.W.T., during spring: Diets and food availability along ice edges. Canadian Journal of Zoology 58:2120–2140.

Bradstreet, M. S. W., and R. G. B. Brown. 1985. Feeding ecology of the Atlantic Alcidae. Pages 263–318 *in* The Atlantic Alcidae: The Evolution, Distribution and Biology of the Auks Inhabiting the Atlantic Ocean and Adjacent Water Areas (D. N. Nettleship and T. R. Birkhead, Eds.). Academic Press, New York.

Broughton, J. M. 1994. Size of the bursa of Fabricius in relation to gonad size and age in Laysan and Black-footed albatrosses. Condor 96:203–207.

Burger, A. E., and J. F. Piatt. 1990. Flexible time budgets in breeding Common Murres: Buffers against variable prey abundance. Pages 71–83 *in* Auks at Sea (S. G. Sealy, Ed.). Studies in Avian Biology, no. 14.

Burger, A. E., and M. Simpson. 1986. Diving depths of Atlantic Puffins and Common Murres. Auk 103:828–830.

Burger, A. E., R. P. Wilson, D. Garnier, and M.-P. T. Wilson. 1993. Diving depths, diet, and underwater foraging of Rhinoceros Auklets in British Columbia. Canadian Journal of Zoology 71:2528–2540.

Cannon, D. Y. 1987. Marine Fish Osteology: A Manual for Archaeologists. Archaeology

Press, Simon Fraser University, Burnaby, British Columbia.

CROLL, D. A. 1990. Physical and biological determinants of the abundance, distribution, and diet of the Common Murre in Monterey Bay, California. Pages 139–148 *in* Auks at Sea (S. G. Sealy, Ed.). Studies in Avian Biology, no. 14.

CROLL, D. A., A. J. GASTON, A. E. BURGER, AND D. KONNOFF. 1992. Foraging behavior and physiological adaptation for diving in Thick-billed Murres. Ecology 73:344–356.

DAVOREN, G. K., AND A. E. BURGER. 1999. Differences in prey selection and behaviour during self-feeding and chick provisioning in Rhinoceros Auklets. Animal Behaviour 58:853–863.

DICK, M. H., AND I. M. WARNER. 1982. Pacific sand lance, *Ammodytes hexapertus* Pallas, in the Kodiak island group, Alaska. Syesis 15: 43–50.

FIELD, L. J. 1988. Pacific sand lance, *Ammodytes hexapterus,* with notes on related *Ammodytes* species. Pages 15–33 *in* Species Synopses: Life Histories of Selected Fish and Shellfish of the Northeast Pacific and Bering Sea (N. J. Wilimovsky, L. S. Incze, and S. J. Westrheim, Eds.). Washington Sea Grant Program and Fisheries Research Institute, University of Washington, Seattle.

FRESH, K. L. 1979. Distribution and abundance of fishes occurring in the nearshore surface waters of northern Puget Sound, Washington. M.S. thesis, University of Washington, Seattle.

GASTON, A. J., AND M. S. W. BRADSTREET. 1993. Intercolony differences in the summer diet of Thick-billed Murres in the eastern Canadian arctic. Canadian Journal of Zoology 71:1831–1840.

GASTON, A. J., AND S. B. C. DECHESNE. 1996. Rhinoceros Auklet (*Cerorhinca monocerata*). *In* The Birds of North America, no. 212 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

GASTON, A. J., AND D. G. NOBLE. 1985. The diet of Thick-billed Murres (*Uria lomvia*) in west Hudson Strait and northeast Hudson Bay. Canadian Journal of Zoology 63:1148–1160.

GIRSA, I. I., AND A. N. DANILOV. 1976. The defensive behavior of the White Sea sand lance *Ammodytes hexapterus*. Journal of Ichthyology 16:862–865.

GROSSE, D. J., AND D. E. HAY. 1988. Pacific herring, *Clupea harengus pallasi*, in the northeast Pacific and Bering Sea. Pages 34–54 *in* Species Synopses: Life Histories of Selected Fish and Shellfish of the Northeast Pacific and Bering Sea (N. J. Wilimovsky, L. S. Incze, and S. J. Westrheim, Eds.). Washington Sea Grant Program and Fisheries Research Institute, University of Washington, Seattle.

GROVER, J. J., AND B. L. OLLA. 1983. The role of the Rhinoceros Auklet (*Cerorhinca monocerata)* in mixed-species feeding assemblages of seabirds in the Strait of Juan de Fuca, Washington. Auk 100:979–982.

HALLEY, D. J., N. HARRISON, A. WEBB, AND D. R. THOMPSON. 1995. Seasonal and geographical variations in the diet of Common Guillemots *Uria aalge* off western Scotland. Seabird 17: 12–20.

HARRIS, M. P., AND T. R. BIRKHEAD. 1985. Breeding ecology of the Atlantic Alcidae. Pages 155–204 *in* The Atlantic Alcidae: The Evolution, Distribution and Biology of the Auks Inhabiting the Atlantic Ocean and Adjacent Water Areas (D. N. Nettleship and T. R. Birkhead, Eds.). Academic Press, New York.

HART, J. L. 1973. Pacific Fishes of Canada. Fisheries Research Board of Canada, Ottawa.

HATCH, S. A., P. M. MEYERS, D. M. MULCAHY, AND D. C. DOUGLAS. 2000. Seasonal movements and pelagic habitat use of murres and puffins determined by satellite telemetry. Condor 102:145–154.

HILTON, G. M., D. C. HOUSTON, AND R. W. FURNESS. 1998. Which components of diet quality affect retention time of digesta in seabirds. Functional Ecology 12:929–939.

HILTON, G. M., G. D. RUXTON, R. W. FURNESS, AND D. C. HOUSTON. 2000. Optimal digestion strategies in seabirds: A modeling approach. Evolutionary Ecology Research 2:207–230.

HOBSON, E. S. 1986. Predation on the Pacific sand lance, *Ammodytes hexapterus* (Pisces: Ammodytidae), during the transition between day and night in southeastern Alaska. Copeia 1986:223–226.

HOURSTON, A. S. 1959. Effects of some aspects of environment on the distribution of juvenile herring in Barkley Sound. Journal of Fisheries Research Board of Canada 16:283–308.

LESCHNER, L. L. 1976. The breeding biology of the Rhinoceros Auklet on Destruction Island.

M.S. thesis, University of Washington, Seattle.

MAHAFFY, M. S., D. R. NYSEWANDER, K. VERMEER, T. R. WAHL, AND P. E. WHITEHEAD. 1994. Status, trends, and potential threats related to birds in the Strait of Georgia, Puget Sound and Juan de Fuca Strait. Pages 256–281 in Review of the Marine Environment and Biota of Strait of Georgia, Puget Sound and Juan de Fuca Strait (R. C. H. Wilson, R. J. Beamish, F. Aitkens, and J. Bell, Eds.). Canadian Technical Report of Fisheries and Aquatic Sciences, no. 1948.

MANUWAL, D. A., T. R. WAHL, AND S. M. SPEICH. 1979. The seasonal distribution and abundance of marine bird populations in the Strait of Juan de Fuca and Northern Puget Sound in 1978. National Oceanic and Atmospheric Administration, Technical Memorandum ERL MESA-44.

MATTHEWS, D. R. 1983. Feeding ecology of the Common Murre, Uria aalge, off the Oregon Coast. M.S. thesis, University of Oregon, Eugene.

MELVIN, E. F., AND L. L. CONQUEST. 1996. Reduction of seabird bycatch in salmon drift gillnet fisheries. 1995 Sockeye/Pink Salmon fishery final report. Washington Sea Grant Program, Seattle.

MELVIN, E. F., L. L. CONQUEST, AND J. K. PARRISH. 1997. Seabird bycatch reduction: New tools for Puget Sound drift gillnet salmon fisheries. 1996 sockeye and 1995 chum salmon test fisheries final report. Washington Sea Grant Program, Seattle.

MELVIN, E. F., AND J. K. PARRISH. 2001. Seabird Bycatch: Trends, Roadblocks and Solutions. University of Alaska Sea Grant Program, Publication AK-SG-01-01.

MELVIN, E. F., J. K. PARRISH, AND L. L. CONQUEST. 1999. Novel tools to reduce seabird bycatch in coastal gillnet fisheries. Conservation Biology 13:1386–1397.

MORROW, J. E. 1979. Preliminary keys to otoliths of some adult fishes of the Gulf of Alaska, Bering Sea, and Beaufort Sea. National Oceanic and Atmospheric Administration Technical Report, National Marine Fisheries Service Circular, no. 420.

NUR, N., AND W. J. SYDEMAN. 1999. Demographic processes and population dynamic models of seabirds: Implications for conservation and restoration. Pages 149–188 in Current Ornithology, vol. 15 (V. Nolan, Jr., E. D. Ketterson, and C. F. Thompson, Eds.). Plenum Press, New York.

OGI, H., AND T. TSUJITA. 1973. Preliminary examination of stomach contents of murres (Uria spp.) from the eastern Bering Sea and Bristol Bay, June–August, 1970 and 1971. Japanese Journal of Ecology 23:201–209.

PENTTILA, D. E. 1995. Investigations of the spawning habitat of the Pacific sand lance, Ammodytes hexapterus, in Puget Sound. Pages 855–859 in Puget Sound Research 1995 Proceedings, vol. 2. Session 8C: Fish Population Assessment Methods and Status and Trends. Puget Sound Water Quality Authority, Olympia, Washington.

PIATT, J. F. 1990. The aggregative response of Common Murres and Atlantic Puffins to schools of capelin. Pages 36–51 in Auks at Sea (S. G. Sealy, Ed.). Studies in Avian Biology, no. 14.

RICHARDSON, F. 1961. Breeding biology of the Rhinoceros Auklet on Protection Island, Washington. Condor 63:456–473.

ROBARDS, M. D., M. F. WILLSON, R. H. ARMSTRONG, AND J. F. PIATT, EDS. 1999. Sand lance: A review of biology and predator relations and annotated bibliography. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Research Paper 521.

SANFORD, R. C., AND S. W. HARRIS. 1967. Feeding behavior and food-consumption rates of a captive California Murre. Condor 69:298–302.

SCOTT, J. M. 1990. Offshore distributional patterns, feeding habits, and adult–chick interactions of the Common Murre in Oregon. Pages 103–108 in Auks at Sea (S. G. Sealy, Ed.). Studies in Avian Biology, no. 14.

SEALY, S. G. 1973. Interspecific feeding assemblages of marine birds off British Columbia. Auk 90:796–802.

SOKAL, R. R., AND F. J. ROHLF. 1995. Biometry, 3rd ed. W.H. Freeman, New York.

SWENNEN, C., AND P. DUIVEN. 1977. Size of food objects of three fish-eating seabird species: Uria aalge, Alca torda, and Fratercula arctica (Aves, Alcidae). Netherlands Journal of Sea Research 11:92–98.

THOMPSON, C. W., M. L. WILSON, D. J. PIERCE, AND D. DEGHETTO. 1998. Population characteristics of Common Murres and

Rhinoceros Auklets entangled in gillnets in Puget Sound, Washington, from 1993 to 1994. Northwestern Naturalist 79:77–91.

VERMEER, K. 1983. Marine bird populations in the Strait of Georgia: Comparison with the west coast of Vancouver Island. Canadian Technical Report of Hydrography and Ocean Sciences, no. 19.

VERMEER, K. 1993. The diet of birds as a tool for monitoring the biological environment. Pages 41–50 *in* The Ecology, Status, and Conservation of Marine and Shoreline Birds on the West Coast of Vancouver Island (K. Vermeer, R. W. Butler, and K. H. Morgan, Eds.). Canadian Wildlife Service Occasional Paper, no. 75.

VERMEER, K., S. G. SEALY, AND G. A. SANGER. 1987. Feeding ecology of Alcidae in the eastern north Pacific Ocean. Pages 189–227 *in* Seabirds: Feeding Ecology and Role in Marine Ecosystems (J. P. Croxall, Ed.). Cambridge University Press, Cambridge.

WAHL, T. R., AND S. M. SPEICH. 1994. Distribution of foraging Rhinoceros Auklets in the Strait of Juan de Fuca, Washington. Northwestern Naturalist 75:63–69.

WILKINSON, L. 1992. SYSTAT for Windows: Statistics, version 5. Systat, Evanston, Illinois.

WILSON, U. W., AND D. A. MANUWAL. 1986. Breeding biology of the Rhinoceros Auklet in Washington. Condor 88:143–155.

WOOTTON, R. J. 1976. The Biology of the Sticklebacks. Academic Press, London.

Associate Editor: A. E. Burger