Chapter 22

Marbled Murrelet Food Habits and Prey Ecology

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Abstract: Information on food habits of the Marbled Murrelet (*Brachyramphus marmoratus*) was compiled from systematic studies and anecdotal reports from Alaska to California. Major differences between the winter and summer diets were apparent, with euphausiids and mysids becoming more dominant during winter and spring. The primary invertebrate prey items were euphausiids, mysids, and amphipods. Small schooling fishes included sand lance, anchovy, herring, osmerids, and seaperch. The fish portion of the diet was most important in the summer and coincided with the nestling and fledgling period. Murrelets are opportunistic feeders, and interannual changes in the marine environment can result in major changes in prey consumption. Site-specific conditions also influence the spectrum and quantity of prey items. More information on food habits south of British Columbia is needed. Studies on the major prey species of the murrelet and relationships between other seabirds and these prey are briefly summarized. Short-term phenomena such as El Niño events would not be expected to adversely affect murrelet populations over the long term. However, cumulative impacts in localized areas, especially in conjunction with El Niño events, could cause population declines and even extirpation.

An understanding of Marbled Murrelet (*Brachyramphus marmoratus*) food habits is needed for effective conservation of this threatened seabird. Many seabirds are known to be affected by prey availability, though human activities induce and compound impacts (Croxall 1987: 377–378; Furness and Monaghan 1987: 35–45, 98–99; Gaston and Brown 1991; Jones and DeGange 1988; Tyler and others 1993). Ainley and Boekelheide (1990: 373–380) discuss the interplay of factors affecting seabird reproduction and total population size, especially as related to different marine systems.

The dramatic loss of old-growth forest nesting habitat (Marshall 1988b) has resulted in a fragmented distribution of the murrelet at sea, especially during the breeding season (Carter and Erickson 1988, Piatt and Ford 1993). Proximity of nesting habitat to an oceanic prey base is important for energetic reasons (Cody 1973, Sealy 1975c, Carter and Sealy 1990), but the bird's capabilities are not understood, and fluctuations in prey populations and variability in prey distribution have not been studied relative to murrelet nesting success or inland distribution. Nevertheless, much of the work on food habits conducted thus far is useful for management purposes and can be used to direct further research.

Six systematic studies on food habits of the murrelet have been conducted in North America. Two occurred during the breeding season in British Columbia (Carter 1984, Sealy 1975c) and one in the non-breeding season (Vermeer 1992). In Alaska, two studies have been conducted in the non-breeding season (Krasnow and Sanger 1982, Sanger 1987b), and one took place during the breeding season (Krasnow and Sanger 1982). These studies form the basis for much of the knowledge of murrelet food habits and are discussed below along with anecdotal information on murrelet diet.

Recent genetic analysis has indicated that the North American Marbled Murrelet warrants full specific status (Friesen and others 1994a). For this reason, and since this chapter was written primarily to aid in management action and recovery planning in North America, information on the diet of the Long-billed Murrelet (*Brachyramphus marmoratus perdix*) has been omitted.

Overall, murrelet food habits in the Gulf of Alaska and British Columbia have received the most attention. Very little information is available on food habits of murrelets in Washington, Oregon, or California, and systematic stomach analyses have never been conducted in these states.

Methods

Because so few studies with large sample sizes have been conducted and the geographic scope of the studies to date is limited, an attempt was made to assemble information on food habits from Alaska to California, even though many of the records are anecdotal or represent field studies with small sample sizes. In addition to a literature review, murrelet biologists from Alaska to California were contacted for information.

An attempt was made to separate adult and nestling food items and to distinguish between foods used in the breeding and non-breeding seasons. However, in some cases the researcher's "winter" collection period continued into the early part of the breeding season (March and April), and the data were not analyzed separately. Also, at times the age class of the murrelet specimens was not stated in the literature. Even if such information were known, the small sample sizes, large geographic differences, and separation of time scales would confound the interpretation of results. Prior to this work, four summaries of murrelet diet were produced (Ainley and Sanger 1979, Ewins and others 1993, Sanger 1983, Carter 1984).

Results

Systematic Studies of Food Habits

Sealy (1975c)

Sealy (1975c) was the first to systematically study murrelet feeding ecology, along with work on the diet of the Ancient Murrelet (*Synthliboramphus antiquus*) near Langara Island, British Columbia. Langara Island is part of the Queen Charlotte Islands and is approximately 500 kilometers

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northwest of Vancouver Island. The study spanned two breeding seasons (1970 and 1971), and 86 adult and subadult Marbled Murrelets were collected between March 25 and August 10 (years combined). The diets were essentially the same for both sexes, and samples from subadults and adults were identical, so the data were pooled for a total sample of 75 individuals. Additionally, six newly fledged murrelets were taken between July 10 and August 4, 1971, and their food habits were analyzed separately. The percentage of murrelets collected that contained prey ranged from 87 to 100 percent.

Sand lance (*Ammodytes hexapterus*) made up 67 percent of the food items in the diet of the adults and subadults. Euphausiids were the next most important food item and contributed 27 percent of the items. Two species of euphausiids were consumed, *Euphausia pacifica* and *Thysanoessa spinifera*, with relative importance values of 2 percent and 25 percent, respectively. The next most important food item was the viviparous seaperch (*Cymatogaster aggregata*), with a value of 3 percent. Overall, sand lance, euphausiids, seaperch, scorpaenids, and osmerids made up 98 percent of the murrelet diet. Including the less common food items which occurred in very small amounts, at least nine different types of prey were identified (*table 1*).

The six samples of newly fledged young selected different prey than adult/subadult murrelets (*table 1*). Sand lance still dominated the diet at 65 percent (similar to 67 percent for adult/subadult murrelets), but the seaperch was the next most important prey species, rather than euphausiids, with a value of 35 percent. The euphausiid, *T. spinifera*, and amphipods made up trace amounts of the remainder of the fledgling diet.

The difference in adult and juvenile diets can be partially explained by looking at the difference in abundance of prey items taken by the adult/subadult murrelets over the course of a breeding season. The euphausiid, *T. spinifera*, was found more commonly in the adult/subadult diet during the mid-April to mid-May period and was more important than the sand lance at this time, but euphausiids diminished greatly in the diet after the early part of the breeding season. However, *T. spinifera* remained important in the diet of adult Ancient Murrelets through mid-July when the study concluded. Sealy attributed this difference in diet to the offshore movement of *E. pacifica* (affinity for deeper water than *T. spinifera*) and, to some extent, offshore movement of *T. spinifera* as the spring progressed and water temperature rose. He also attributed the diet change to reduced abundance of *T. spinifera* due to loss of females after reproduction. Additionally, he noted that adult Ancient Murrelets feed further offshore than Marbled Murrelets or juvenile Ancient Murrelets, and he believed the food supply of the Ancient Murrelet was spotty and unpredictable.

Sealy tested for a measurable change in prey availability mid-summer by examining the stomach contents of 13 individuals of seven species, including the Ancient and Marbled Murrelet, from six mixed-species feeding assemblages. Between 9 May and 26 June 1971 he conducted plankton hauls where collected birds had been foraging. The results indicated that only *Thysanoessa* was available and taken by those individuals examined in May, and later samples in June found only *Ammodytes* available and being consumed. He concluded that fishes such as *Cymatogaster* and *Ammodytes* tend to spend the winter and early spring in midwater offshore, but migrate to the surface and move inshore in late spring, thus possibly becoming available to murrelets at this time.

Plankton hauls made in 1971 also indicated that the murrelets were more selective in their feeding habits when compared to prey availability (Sealy 1975c). Organisms such as ctenophores, amphipods, and polychaetes were obtained in the plankton hauls, but none of these organisms were found in the food samples analyzed. Zooplankton sampling by Project NorPac (Dodimead 1956) during summer 1955 (primarily in August) resulted in a similar difference in prey availability; copepods were by far the most numerous organisms with a total volume of more than 65 percent, while euphausiids composed less than 10 percent of the total volume (LeBrasseur 1956).

Sealy (1975c) concluded that murrelets seldom feed more than 500 m from shore, usually in water less than 30 m deep. His work demonstrated that euphausiids made up only a small part of the overall diet during the breeding season, but were dominant during the early part of the breeding season. He thought the breeding season was possibly ultimately controlled by the cycles of abundance of fishes near shore, especially the sand lance, which were taken by the murrelet in great quantities in the study area.

Krasnow and Sanger (1982)

Krasnow and Sanger (1982) collected murrelets at sea in the vicinity of Kodiak Island in the winter of 1976/1977. They collected 18 murrelets (all with food) between December 1976 and April 1977 at Chiniak Bay, a large bay on the northeast end of Kodiak Island; a second sample of 19 murrelets (16 with food) was collected from Chiniak in February 1978. Two other sites were sampled during the breeding season of 1978. At Izhut Bay, a small bay north of Chiniak Bay, Krasnow and Sanger collected 34 murrelets (25 with food) between April and August 1978 and from Northern Sitkalidak Strait, which is located on the southeast end of Kodiak, they collected 26 murrelets (17 with food) between May and August 1978. The percentage of murrelets collected which contained prey ranged from 65 to 100 percent.

Krasnow and Sanger calculated an Index of Relative Importance (IRI) value for the foods consumed by murrelets according to Pinkas and others (1971). During the 1976/1977 winter, fish, primarily of the family osmeridae, were the most important prey, followed by euphausiids of the genus *Thysanoessa*, and mysids (*table 2*). A total of 11 different prey items were identified (*table 2*), compared to nine from Sealy's (1975c) breeding season study (*table 1*).

Table 1—Marbled Murrelet prey items from systematic studies and anecdotal observations, Alaska to California

	Grinnell (1897) and (1910)	Simons (1980)	Sanger (1983)	Munro and Clemens (1931)	Sealy (1975c)	Sealy (1975c)	Carter (1984)	Carter (1984)	Carter (1984)	Carter (1984)	Mahon and others (1992)	Mahon and others (1992)	Guiguet (1956)	Guiguet 1956; Guiguet [1950] *in* Carter (1984)	Vermeer (1992)	Jones and Dechesne (1994)	Brooks (1928); Carter and Sealy (1986)	G. Hunt, pers. comm.	Cody (1973)	Cody *in* Carter (1984)	Strong and others (1993)	K. Nelson, pers. comm.	Beck (1910)	P.R.Kelly (pers. comm.) *in* Carter and Erckson (1988)	Ralph and others (1990)	Naslund (1993a)
Location[1]	AL	AL	AL	BC	BC	BC	BC	BC	BC	BC	BC	BC	BC	BC	BC	BC	AL–OR	WA	WA	WA	OR	OR	CA	CA	CA	CA
Sample size[2]	—	1	129	4	75	6	71	11	—	5	—	—	—	—	25	—	5	—	—	—	6	—	~19	10	1	3
Season of collection/ observation[3]	BR	BR	A	NB	BR	BR	BR	BR	BR	NB	BR	BR	BR	BR	NB	BR	BR	BR	BR	BR	BR	BR	NB	NB	BR	BR
Age class of murrelets[4]	U	N	U	A	A	J	A	J	N	U	U	N	U	N	U	N	A	U	N	N	N	N	U	U	N	N
Prey species[5] — Invertebrates																										
Unid. Nereidae (Polychaeta)			I																							
Littorina sitkana (Gastropoda)			I																							
Unid. Gastropoda			I																							
Mytilus edulis (Bivalvia)			I																							
Loligo opalescens (Cephalopoda)					I					X																
Unid. Cephalopoda			I																							
Unid. Mollusca	A																									
Acanthomysis sp. (Mysidae)			O																							
Neomysis rayii (Mysidae)			I																							
Neomysis sp. (Mysidae)			I																							
Unid. mysid			I	A																						

continues

Table 1, continued

	Grinnell (1897) and (1910)	Simons (1980)	Sanger (1983)	Munro and Clemens (1931)	Sealy (1975c)	Sealy (1975c)	Carter (1984)	Carter (1984)	Carter (1984)	Carter (1984)	Mahon and others (1992)	Mahon and others (1992)	Guiguet (1956)	Guiguet 1956; Guiguet [1950] in Carter (1984)	Vermeer (1992)	Jones and Dechesne (1994)	Brooks (1928); Carter and Sealy (1986)	G. Hunt, pers. comm.	Cody (1973)	Cody in Carter (1984)	Strong and others (1993)	K. Nelson, pers. comm.	Beck (1910)	P.R.Kelly (pers. comm.) in Carter and Erckson (1988)	Ralph and others (1990)	Naslund (1993a)
Atylus tridens (Amphipoda)						I																				
Unid. Gammarid (Amphipoda)			I																							
Thysanoessa inermis (Euphausiid)			O																							
T. raschii (Euphausiid)			I																							
T. spinifera (Euphausiid)			I		X	I									O											
Thysanoessa sp. (Euphausiid)			I																							
Euphausia pacifica (Euphausiid)					O										O											
Unid. Euphausiid			I	A									A		I											
Pandalus borealis (Decapod)			I																							
Unid. Decapod			I		I																					
Unid. Chaetognatha			I																							
Prey species[5] — Fish																										
Clupea harengus (Clupeidae)							X	X	A	O		A		A	X			P				P				
Sardinops sagax (Clupeidae)																							A			
Unid. Clupeidae																										P
Engraulis mordax (Engraulididae)							I		A										A	A				A	A	P

continues

Table 1, continued

	Grinnell (1897) and (1910)	Simons (1980)	Sanger (1983)	Munro and Clemens (1931)	Sealy (1975c)	Sealy (1975c)	Carter (1984)	Carter (1984)	Carter (1984)	Carter (1984)	Mahon and others (1992)	Mahon and others (1992)	Guiguet (1956)	Guiguet 1956; Guiguet [1950] in Carter (1984)	Vermeer (1992)	Jones and Dechesne (1994)	Brooks (1928); Carter and Sealy (1986)	G. Hunt, pers. comm.	Cody (1973)	Cody in Carter (1984)	Strong and others (1993)	K. Nelson, pers. comm.	Beck (1910)	P.R.Kelly (pers. comm.) in Carter and Erckson (1988)	Ralph and others (1990)	Naslund (1993a)
Mallotus villosus (Osmeridae)		P	X																							
Thaleichthys pacificus (Osmeridae)	P																									
Unid. Osmeridae			O		I																A	A				A
Onchorhynchus sp./ *Salmo* sp. (Salmonidae)																	A									
Strongylura exilis (Belonidae)																							P			
Theragra chalcogramma (Gadidae)			I																							
Unid. Gadidae (Codfishes)			I																							
Trichodon trichodon (Trichodontidae)			I																							
Scorpaenidae (Rockfishes)					I		I	I		O																
Cymatogaster aggregata (Embiotocidae)				P	O	O						A														
Stichaeidae (Pricklebacks)					I																					
Ammodytes hexapterus (Ammodytidae)			X		X	X	O	O	A	I	A	A	A	A		A			A		A	A		A		
Unid. Fish	A		O	A[6]																			A			

[1] AL = Alaska, BC = British Columbia, WA = Washington, OR = Oregon, CA = California
[2] — = Unknown or not recorded
[3] BR = Breeding, NB = Non-Breeding, A = All seasons
[4] A = Adult/Subadult, J = Juvenal, N = Nestling, U = Unknown
[5] X = Major, O = Minor, I = Incidental, P = Possible, A = Anecdotal observation
[6] Larval fish

Table 2—Comparison of winter diet of Marbled Murrelets in Chiniak Bay, Alaska, between December 1976-April 1977, and February 1978[a]

	Year	
Prey	1976/1977	1978
Nereidae	3[b]	0
Chaetognatha	1	0
Mysidacea	23	447
Acanthomysis sp.	4	10,548
Neomysis sp.	0	870
N. rayii	2	27
Thysanoessa sp.	74	0
T. inermis	1,169	0
T. spinifera	5	0
T. raschii	0	4
Gammaridea	0	58
Decapoda	0	8
Pandalidae	0	6
Pandalus goniurus	0	4
Osteichthyes	3	62
Osmeridae	1,584	33
Mallotus villosus	526	41
Theragra chalcogramma	0	4
	n = 18	*n* = 16

[a] Data from Krasnow and Sanger (1982)

[b] Values are Index of Relative Importance values calculated after Pinkas and others (1971).

In contrast to the results of Sealy (1975c), no *Ammodytes* were present, but, similar to Sealy's (1975c) study, *Thysanoessa* was an important prey item.

The results from the February 1978 collections were extremely different from the 1976/1977 winter data. Mysids dominated the prey items with a cumulative IRI value of 11,892 (*table 2*). Osteichthyes were second, followed by gammarids and capelin (*Mallotus villosus*). A total of 13 different prey items were identified (*table 2*). Once again, no *Ammodytes* were noted, and even *Thysanoessa* was reduced to an IRI value of 4. Sealy's (1975c) breeding period study did not detect mysids and gammarids, but these prey items appear to be more important in the winter diet of murrelets, at least in the Gulf of Alaska (Sanger 1987b, Sanger and Jones 1982). The lack of *Thysanoessa* consumption in February 1978 by the murrelets is particularly interesting in light of Sealy's (1975c) work. Krasnow and Sanger (1982) reported that murrelets fed primarily in shallow water but obtained their prey throughout the water column. Sanger (1987b) noted that the ability of murrelets to forage at least part of the time near the bottom assures a broader trophic spectrum than a food supply originating with phytoplankton productivity in the water column alone.

The reduction of capelin in the winter diet of murrelets between the study periods may be due to the dynamic nature of capelin populations. Because capelin live only 3 or 4 years and most spawn only once, poor recruitment of a given year class can lead to cycles of abundance and near absence [Warner and Dick *in* Krasnow and Sanger (1982)]. Fisheries data indicated that the distribution of capelin was different in the 2 years, with most fish being caught in deep troughs in 1978 [Rogers and others *in* Krasnow and Sanger (1982)]. Additionally, fewer capelin and more sand lance were fed to Black-legged Kittiwake (*Rissa tridactyla*) chicks in Northern Sitkalidak Strait during 1978 than in 1977. Productivity of kittiwakes declined from 0.74 young fledged per nest attempt to 0.17, suggesting that the availability of food was depressed below some "critical level" [Baird and Hatch *in* Krasnow and Sanger (1982)]. Productivity of kittiwakes in Chiniak Bay also decreased, from 1.23 young fledged per nest attempt in 1977 to 0.77 in 1978 [Nysewander and Barbour *in* Krasnow and Sanger (1982)]. Food samples were not collected at the breeding colonies of kittiwakes in Chiniak Bay in 1978, and thus the assumption that fewer capelin were brought to chicks than during the previous years could not be substantiated.

If euphausiids were scarce or, for some reason, unavailable to murrelets in early 1978 in Chiniak Bay, then the ability of the murrelet to feed so heavily on detritivores such as mysids and gammarids likely demonstrates prey-switching capability. This adaptive and opportunistic behavior illustrates the result of natural selection pressure due to dynamic prey populations. Alternatively, two factors, small sample size and a difference in the collection period (5 months compared to 1 month), could be complicating the results. However, given the information on kittiwake reproduction and capelin being found in deeper waters cited above, it would appear that changes in the marine food web in Chiniak Bay between years and prey-switching behavior by the murrelet are more plausible explanations.

The results of Krasnow and Sanger's (1982) study of breeding-season diet at Izhut Bay and Northern Sitkalidak Strait in 1978 pointed to the importance of local differences in the relative availability of major prey species within the same year. The diets from the two different study areas included a high proportion of unidentified osteichthyes (*table 3*), with ten different prey items identified in the summer diet, comparing with 9 from Sealy (1975c). Euphausiids were more common in the murrelet diet at northern Sitkalidak Strait. For the murrelets and most other seabird species in the Kodiak area, distinct seasonal trends were apparent from spring through late summer 1978. Marbled Murrelets, Tufted Puffins (*Fratercula cirrhata*), Sooty Shearwaters (*Puffinus griseus*), and Black-legged Kittiwakes exploited a similar suite of prey. Sand lance and euphausiids were taken during spring, capelin during early summer, and sand lance during late summer. The authors attributed this chronology to the probable seasonal occurrence and distribution of prey as did Sealy (1975c) and Carter (1984) in their study areas.

Table 3—Comparison of May 1978 breeding season diet of Marbled Murrelets between Izhut Bay and Northern Sitkalidak Strait, Alaska[a]

Prey	Location	
	Izhut Bay	Northern Sitkalidak Strait
Crustacea	60[b]	0
Thysanoessa inermis	0	18,910
Osteichthyes	316	82
Osmeridae	326	0
Mallotus villosus	5,957	190
	n = 3	*n* = 4

[a] Data from Krasnow and Sanger (1982)

[b] Values are Index of Relative Importance values calculated after Pinkas and others (1971)

The difference between the two areas in the May diet (*table 3*) may be due to the small sample sizes or may represent a local difference in prey abundance as discussed above relative to winter diet. The two study areas showed similarity in murrelet diet in June, with fish (primarily capelin) the most important food item. The July samples indicated the importance of sand lance and fish in murrelet diet during that period: three birds collected at Izhut Bay had only sand lance in their stomachs, while four birds collected at Sitkalidak were full of sand lance and other unidentified osteichthyes.

Sanger (1983)

Sanger's compilation of data from throughout the Gulf of Alaska, and across all seasons, provides an overview of the broad spectrum of the murrelet's diet (*table 1*). Data were derived from multiple Outer Continental Shelf Environmental Assessment Program (OCSEAP) studies (including Krasnow and Sanger 1982, Sanger and Jones 1982) and from the National Marine Fisheries Service (*n* = 129). At least 16 prey species were identified. This broad spectrum of prey species from different trophic levels is a good indication that the murrelet is an opportunistic feeder, though preferences have been documented (Sealy 1975c). Generally, murrelets seem to prefer euphausiids in spring and fish in summer though prey availability and energetic requirements during these seasons are also important factors in prey selection (Carter and Sealy 1990, Cody 1973, Sealy 1975c).

Additionally, "food-chain pathways that include detritus may result in a more stable food supply than non-detrital food chains. This could be reflected in demersal-benthic feeders like Pelagic Cormorants [*Phalacrocorax pelagicus*] and Pigeon Guillemots [*Cepphus columba*] showing stable productivity over the years, compared with midwater and surface feeders. Winter survival of species like Common Murres [*Uria aalge*] and Marbled Murrelets may be enhanced by their ability to alter their 'normal' diet of pelagic fishes to include demersal crustaceans, thus seasonally linking themselves to a detrital-based food chain" (Sanger 1987a).

Sanger (1987b)

One last example of the importance of local conditions on murrelet diet from the OCSEAP work in Alaska comes from a summary of work done in Kachemak Bay during the winter of 1978 (Sanger 1987b). Twenty-one murrelets were collected from January to April 1978, and 18 stomachs were used for the analysis. Capelin and osmerids dominated the diet, followed by euphausiids (*Thysanoessa* sp.), mysids, unidentified gammarid amphipods, and sand lance. Compared to the work of Krasnow and Sanger (1982) in Chiniak Bay, euphausiids were more important, and sand lance were taken. Thus, although the sample sizes are similar, the relative importance of prey species is variable. This disparity is another example of the importance of local and interannual conditions in determining murrelet food habits.

Carter (1984)

Carter's intensive study occurred in Barkley Sound, on the southwest coast of Vancouver Island. Field work was conducted from 10 May to 7 September 1979, 18–19 December 1979, and 8 June to 13 October 1980. Eighty-seven murrelets were obtained during the study and examined for diet information. Carter (1984) noted that small fish larvae (<31 mm) were apparently digested quickly, and therefore this size class was under-represented in the results. Food samples from both sexes were taken throughout the day in both years and were combined for analysis. Carter also separated the diet of breeding, molting, hatching-year, and winter birds and calculated a relative importance value in the same way of Sealy (1975c), though he referred to this percent value as frequency.

Breeding adults fed primarily on sand lance and Pacific herring (*Clupea harengus*), including larval and juvenile fish (*table 1*). Molting and hatching-year birds also fed primarily on herring and sand lance, and four juvenile northern anchovy (*Engraulis mordax*) were found in the stomach of one molting bird. Carter (1984) noted that molting murrelets consumed more herring (90 percent) than sand lance (7 percent), and the same was true for the hatching-year murrelets, with herring consumption at 81 percent and sand lance at 13 percent. By contrast, the breeding murrelets consumed more sand lance (63 percent) and less herring (36 percent) (*table 1*).

In contrast to the work of Sealy (1975c), euphausiids were absent in the diet of murrelets in Barkley Sound. Though Carter's (1984) work began approximately one month later than Sealy's (1975c), euphausiids in minor amounts should have occurred at least in May and throughout the summer at least as a minor component of the diet. Additionally, the overall diversity of prey species in the summer diet of murrelets from Barkley Sound was low (4 different prey items) compared to 9 from Sealy's (1975c) study and 10 from Krasnow and Sanger (1982).

Five murrelets collected in winter had eaten scorpaenid rockfish and squid (*Loligo opalescens*), as well as large juvenile herring and sand lance (*table 1*). Scorpaenids and *Loligo* were also found in the murrelet diet at Langara Island by Sealy (1975c) during the breeding season (*table 1*).

Carter (1984) also made observations at sea of adults holding fish for nestlings; *Ammodytes*, *Clupea*, and *Engraulis* were documented as nestling food (*table 1*).

The importance of herring in the diet of the murrelet in Carter's (1984) study correlates with the local abundance and availability of juvenile herring. He suggested that murrelets fed opportunistically on available prey and noted that juvenile herring were abundant only in localized areas near spawning grounds (Hourston *in* Carter 1984). This conclusion is further strengthened by the work of Vermeer (1992) discussed below.

Vermeer (1992)

Winter food habits of murrelets from Quatsino Sound, British Columbia, were studied for the period from October 1981 through March 1982 (Vermeer 1992). Quatsino Sound is located approximately 270 kilometers northwesterly of Barkley Sound where Carter's (1984) work was conducted.

Twenty-five murrelets were collected, and all birds (100 percent) contained food. Most fish were digested, but Pacific herring were identified in 15 of the 25 murrelets. All invertebrates eaten consisted of euphausiids, of which *T. spinifera* and *E. pacifica* were the main species. The fish portion of the diet constituted 71.2 percent of the wet weight of the prey items, and the invertebrate portion was 28.7 percent; thus, the murrelets ate mostly fish, primarily herring, during the non-breeding season in Quatsino Sound (*table 1*). Sand lance were not consumed, and the diversity of prey items (at least 3) was low compared to that found in the winter diet work by Krasnow and Sanger (1982) and Sanger (1987b).

Vermeer (1992) did point out that the study location has one of the largest herring spawn areas along the west coast of Vancouver Island and that herring spawn constitutes a major food source for piscivorous as well as nonpiscivorous birds, such as diving ducks. The massive presence of herring in March for spawning and the predictable nature of this occurrence has resulted in annual utilization of this resource by many seabirds and other animals (Vermeer 1992). Therefore, it seems apparent that the high use of herring in Vermeer's (1992) study is another example of the opportunistic foraging behavior of the murrelet and another demonstration of the importance of local differences in availability of prey as noted by Krasnow and Sanger (1982). Of further interest, four male murrelets collected in Departure Bay on the southeast coast of Vancouver Island during February and March (in 1928 and 1929) did not contain any identifiable herring in their stomachs even though the study area was also known as a major spawn location for herring during March (Munro and Clemens 1931). Results and implications of the Munro and Clemens (1931) collection effort are described in more detail below.

Freshwater Feeding

The studies described previously were conducted to assess murrelet food habits in the marine environment. To assess the importance of freshwater lakes in the feeding ecology of murrelets, Carter and Sealy (1986) summarized records of year-round use of coastal lakes for the period 1909 to 1984 from Alaska to California. No records were found for California. Three of the 67 records included small collections of murrelets at lakes in British Columbia during late April and early May. Five stomachs of adults were examined, and three were found to contain yearling Kokanee salmon (*Onchorhynchus nerka kennerlyi*), while the fourth contained two fingerling sockeye salmon (*O. nerka*). The examiner of the fifth murrelet, R.M. Stewart, noted, "The stomach was full of small fish which looked like salmon fry" [*Onchorhyncus* or *Salmo* sp.] (Brooks 1928) (*table 1*). Carter and Sealy's (1986) work contains numerous anecdotal sightings of murrelets feeding at inland lakes and references which document many of the lakes as large nurseries for juvenile salmon. The discussion includes evidence for nocturnal feeding by murrelets and winter-time use of inland lakes. The relative lack of inland lakes near known nesting sites south of British Columbia, along with a lack of census effort for murrelets at inland lakes, could lead to an underestimate of the importance of lakes and freshwater fish species as a food source for the murrelet. The effect of the reduction of salmonid stocks on the use of lakes by murrelets is unknown. This aspect of the murrelet's life history needs further investigation throughout its range.

Isotopic Analysis of Diet

Stable carbon and nitrogen isotopic analyses were performed on tissues of Marbled Murrelets collected from July to December 1979 (Carter 1984), in Barkley Sound ($n = 18$), and in June 1985 on Johnston Lake, British Columbia ($n = 3$) (Hobson 1990). Most murrelets showed stable carbon isotopic values (pectoral muscle) between -15.5 and -17.5, and males and females were the same. These values compare favorably to the value of -17.9 for a sample of five *Ammodytes* sp. taken from coastal British Columbia for comparison. However, three individuals, an adult male from Barkley Sound and two adult males from Johnston Lake, differed significantly from the group. On the basis of a model, Hobson concluded that the three individuals had short-term freshwater-derived protein inputs to their diets ranging from 50 to 100 percent. Hobson (1990) suggested that while some murrelets may feed exclusively on freshwater prey for a short but important period of several weeks, freshwater protein did not appear to be a significant long-term dietary component. However, he concluded that he was unable to ascertain the relative importance of freshwater feeding in different murrelet populations without additional analysis. He suggested that tissues from murrelets found dead or collected for other studies be analyzed by isotopes of stable carbon.

Analysis by isotopes of stable nitrogen cannot be used for separating dietary differences between freshwater and marine protein contributions, because nitrogen isotope ratios in the muscles of fish species in coastal lakes may overlap with those of marine fish (Hobson 1990). Lower trophic-level fish such as fingerling salmonids also overlap with marine invertebrates. Thus, nitrogen isotope analysis may be better suited than carbon to delineating the trophic levels of murrelets and other seabirds. The results of this analysis (Hobson 1990) showed Marbled Murrelets in the middle of a spectrum (10 species) from Dovekies (*Alle alle*) to Pigeon Guillemots; the Marbled Murrelet was between the Ancient Murrelet and the Common Murre. This isotopically intermediate position is consistent with the results of the studies described above which document murrelet consumption of invertebrate prey as well as marine fish. The trophic-level approach also has the value of being less biased against the soft-bodied invertebrates which are not easily detected in conventional studies.

A further analysis of the variability of stable nitrogen isotopes in wildlife showed that tissue can be enriched because of fasting or nutritional stress (Hobson and others 1993). Thus, studies using analysis by stable nitrogen isotopes to infer diet or trophic position must take into account the nutritional history of the individual specimen. Fasting should not be a factor for the murrelet because both sexes incubate the egg and feed the nestling, but nutritional stress could affect the results in a year of severe prey shortage.

Ecological Studies and Anecdotal Information

Alaska

Food habits of the murrelet were described by Bent (1963), "The food of the marbled murrelet seems to consist largely of fish which it obtains by diving in the tide rips and other places where it can find small fry swimming in schools." It appears he derived this information from observations contained in Grinnell (1897) and Grinnell (1910) (*table 1*). In the summer of 1896, during a visit to Sitka Bay, Alaska, Grinnell (1897) noted, "Small fish caught by diving seemed to be the standard article of food, but dissection of the stomachs also showed remains of some small mollusks. A shoal of candle-fish [*Thaleichthys pacificus*] was sure to have among its followers, besides a cloud of Pacific kittiwakes [*Rissa* sp.], several of the Murrelets" (*table 1*). Grinnell (1910: 366) noted fish as a prey item in a collected specimen and during an observation by Joseph Dixon of a foraging murrelet, but the species of fish were not recorded (*table 1*).

Observations at the first documented ground nest of a murrelet indicated capelin as a food source for the nestling (Simons 1980) (*table 1*). An adult murrelet delivered a single fish about 8 cm long. Simons (1980) noted, "The fish *appeared* to be a capelin (*Mallotus* sp.)..." [emphasis added]. This observation would appear valid given the documented importance of capelin in murrelet diet in Alaska (Sanger 1983). Simons (1980) also noted that the pattern of weight gain was variable from days 2 to 12, and he suggested the possibility of multiple feedings. He concluded that predation and the distribution of the food resource were important selective agents acting upon ground-nesting murrelets.

British Columbia

Food habits of "water fowl" during the spawning season of herring in the vicinity of Departure Bay, British Columbia, were studied between 1928 and 1930 (Munro and Clemens 1931). Four male murrelets were collected in late February to mid-March, and the stomachs contained *Cymatogaster*, larval fish, mysids, and schizopods (*table 1*). The archaic group schizopoda included euphausiids and mysids because, superficially, the members of these two orders appeared so similar. These two groups are now separated into different tribes based on characteristics of the carapace and the distinguishing luminescent organs of the euphausiids (Hardy 1965: 171-172).

The results from Munro and Clemens (1931) differ from the winter results of Carter (1984) and Vermeer (1992), in that identifiable herring are absent (*table 1*). This difference could be due to the small sample size. Alternatively, it could result from differences in availability of herring age classes and in herring distribution relative to murrelets, and differences in the magnitude and duration of the herring spawn between the three study areas (McAllister, pers. comm.). A number of herring stocks aggregate close to the spawning area for some time before actually moving on to the grounds to spawn (Lambert 1987).

An anecdotal account of murrelet diet by Guiguet was published in 1956. He spent many summers on zoological exploration in coastal British Columbia and stated that the murrelet "...eats small crustacea such as euphausid [sic] shrimps, and fishes such as the sand launce [sic]...." He also described watching murrelets foraging off the Queen Charlotte Islands in July 1946 and noted, "all were feeding on sand launces [sic]...." When darkness had almost descended that day, the murrelets disappeared inland to the west. Guiguet (1956) noted, "All of them were 'packing feed' in their bills, and the silvery sand launce [sic] showed up in the darkness" (*table 1*).

Between 6 June and 8 August 1991, Mahon and others (1992) conducted 27 at-sea surveys to determine the composition and density of mixed feeding flocks. They observed 126 feeding flocks, 100 of which contained only murrelets and Glaucous-winged gulls (*Larus glaucescens*). Murrelets were seen to feed on schools of sand lance by driving the fish to the surface. First-year sand lances were the only prey identified in feeding flocks (*table 1*). In the evenings, murrelets were seen holding larger sand lance, Pacific herring, and shiner perch as prey for nestlings (*table 1*). The nestling prey items closely match the juvenile diet reported by Sealy (1975c), and two of the nestling items, herring and sand lance, reported by Carter (1984) and Guiguet (1956), respectively.

Additional anecdotal information on nestling food habits in British Columbia comes from a nest which was monitored in summer 1993 (Jones and Dechesne 1994). Sand lance was noted as a prey item for the nestling (*table 1).*

Washington

During the summers of 1968 and 1969, Cody (1973) collected information on seabird breeding activity, prey species, and foraging patterns off the west coast of the Olympic Peninsula in Washington State. Murrelets holding fish before their evening flights inland were observed at close range from a boat. The birds were seen to carry only anchovy (*Engraulis*) and sand lance (*Ammodytes*) in their bills, and it was presumed these fish were for nestlings (Carter and Sealy 1987a) (*table 1*). The murrelets showed great similarity in chick diet with the Common Murre, Tufted Puffin, and Rhinoceros Auklet (*Cerorhinca monocerata*), though smelt (*Hypomesus*) and sea-bass (*Sebastoides*) were also recovered from 54 fish loads for these latter three species of alcids.

Similar to Sealy's (1975c) study of sympatric Ancient and Marbled Murrelets, Cody (1973) concluded that differences in foraging areas at sea reduced interspecific competition between alcids off the west coast of the Olympic Peninsula, though prey species consumed were similar. Lacking specific knowledge of murrelet nesting areas, neither of these researchers were able to compare foraging areas with nesting habitat distribution, though Cody (1973) concluded that the zonation of alcid feeding areas with respect to distance from the nest was the most important factor affecting coexistence. He contrasted this to other studies which have found differences in diet between similar seabird species to be the isolating mechanism. He also pointed out that foraging zonation which is optimal while adults feed nest-bound young is relaxed and expanded when young leave their nests and accompany the parents. Cody (1973) found that murrelets fed within a few kilometers of the shore. He observed that in the evenings they were often seen carrying food within a half kilometer of the Hoh and Quilleute Rivers and that adults and partially-grown, non-flying young were observed close to these same river mouths in August.

Cody presumed these rivers provided transportation for the young murrelets from inland nesting sites (Day and others 1983, Nechaev 1986). The discovery of a young murrelet at a freshwater marsh close to the sea in British Columbia is described by Brooks (1926a). The bird appeared unable to fly, and it was noted that the primaries were in sheaths at their bases and there was a good deal of down on the head, back, and flanks. Another similar young was with it. Brooks (1926a) noted another juvenile murrelet, collected off Langara Island, British Columbia: "...the bases of its quills still in the sheath was taken some 200 yards out to sea...". Young fledglings would consume available prey resources in freshwater environments as they gained sustained flight capabilities and made their way to the ocean (Carter and Sealy 1986). It is thought that the majority of murrelets fledge by direct flight to the ocean (Nelson and Hamer, this volume a). Diving behavior is an escape response and does not necessarily indicate an inability to fly (Carter and Sealy 1987b); however, repeated harassment of the juveniles by Cody (1973) resulted in no flight attempts, though adults would take wing when continually harassed by boat (Cody, pers. comm.).

Additional work by Cody *in* Carter (1984) at the San Juan Islands again revealed anchovy as nestling prey from fish held in the bill by murrelets on the water (*table 1*).

One other observation on murrelet food habits from Washington was provided by Hunt (pers. comm.). He observed murrelets foraging in August in mixed-species flocks in the San Juan Islands. He dip-netted (approximately 7.5 cm mesh) for surface fish in this foraging area and captured only herring (*table 1*).

Oregon

At-sea surveys for murrelets during 1992 off the coast of Oregon resulted in some anecdotal information on nestling food items (Strong and others 1993). A total of six murrelets carrying fish were observed from 15 June to 11 August (*table 1*). The first two observations occurred on 15 June, and the prey type was judged to be "smelt sp." (osmeridae). The next four observations, on 1 August, 2 August, and 11 August (two observations), were of sand lance. On the basis of additional observations of other seabirds with prey over the same time period, the authors thought a switch in prey occurred from smelt in late July to sand lance thereafter.

Video footage from an active nest site in 1992 documented sand lance as nestling food, and during at-sea surveys, observers noted osmerids, sand lance, and a possible herring as nestling food items being held by murrelets (Nelson, pers. comm.) (*table 1*).

California

A report on the population status and conservation problems of the murrelet in California was produced in 1988 as the Department of Fish and Game began gathering information on the species (Carter and Erickson 1988). Field notes from work by R. H. Beck in the vicinity of Point Pinos, Monterey County, were included in Carter and Erickson's (1988) report and are repeated here (Museum of Vertebrate Zoology; see also Beck 1910): "...the Marbled Murrelets yesterday [had in their stomachs] 2, 3, 4, or 5 small sardines [*Sardinops sagax*] about 3 inches long" (November 24, 1910); four days later, 13 murrelets were collected (November 28, 1910), and Beck noted, "Sardines 2 to 3 inches long in stomachs"; then, on February 16, 1911, Beck reported, "A six [inch] needle fish? [*Strongylura exilis*] swallowed by Marbled Murrelet inside bill when picked up fish just caught"; and finally, on March 1, 1911, a Marbled Murrelet was collected with a "...6 1/2 [inch] fish in stomach" (*table 1*).

The reference to the possible needlefish (California needlefish = *Strongylura exilis*) is interesting because the northern distribution limit for this species is San Francisco (Miller and Lea 1972). Carter and Erickson (1988) thought the fish may have been a sand lance.

Carter and Erickson (1988) also reported on the food habits of 10 murrelets which were collected in early fall from northern Monterey Bay in the late 1970's. The murrelets were noted as feeding mainly on anchovy and to a lesser extent on sand lance (*table 1*).

Another instance of anchovy in murrelet diet came from mist netting of murrelets in Redwood National Park for radio-telemetry purposes during summer 1989 (Ralph and others 1990). During this work, on July 3, 1989, one murrelet hit the mist net and bounced out (05:30 p.d.t.), leaving a whole northern anchovy at the base of the net. The anchovy weighed 10.0 grams and was 113 mm in length. It seems most likely that this prey item was destined for a murrelet nestling (*table 1*).

It is unfortunate that systematic studies of murrelet food habits in this region of California did not occur before and after the great sardine fishery (mid 1930 to mid 1940). The anecdotal information from above mirrors the documented change in prey abundance over time, from sardine to anchovy. The interesting history of sardine and anchovy population fluctuations and their fisheries are briefly summarized below under the prey ecology section of this chapter. The fact that murrelets have persisted in the central California region after a decline in the largest fishery in the Western Hemisphere is probably another indication of the opportunistic feeding behavior of the bird. This flexibility in prey choice has probably helped to sustain the murrelet population in this geographic region in spite of massive loss and deterioration of inland nesting habitat.

Anecdotal information on nestling diet was obtained from video footage recorded during observation of an active nest site in Big Basin State Park in the Santa Cruz Mountains (Naslund 1993a). Three fish carried to the nestling were identified (*table 1*). Two of the fish appeared to be either northern anchovy or possibly of the clupeidae. The third fish was judged to be a smelt (osmeridae).

Rockfish make up an important component of seabird diet in California, and if more intensive studies of murrelet diet were conducted it is possible that these fish would be found to be eaten by murrelets (Ainley and others, this volume). Both Sealy (1975c) and Carter (1984) documented scorpaenids in the murrelet's diet (*table 1*).

Food Habits Summary

The sand lance is the most common food of the murrelet across its range (*table 1*). For the fish species, records of sand lance represent 52 percent of the compiled information (11 occurrences per 21 studies/anecdotal observations) on murrelet food habits. The next most commonly recorded species are anchovy and herring at 29 percent, followed by osmerids at 24 percent, and by *Cymatogaster* at 14 percent.

Euphausiids as a group represented 24 percent of the compiled information (*table 1*). They were generally not a dominant component of murrelet diet during the breeding season; however, euphausiids were an important prey source for murrelets in the spring (Sealy 1975c) and during the breeding season in some years (Krasnow and Sanger 1982). Euphausiids were also important during the winter in the Gulf of Alaska (Krasnow and Sanger 1982) and in British Columbia (Vermeer 1992). Mysids and gammarids were another component of murrelet diet, especially in winter (Krasnow and Sanger 1982, Munro and Clemens 1931, Sanger 1987b).

Studies under the OCSEAP program revealed the importance of seasonal and interannual variation in prey abundance (Krasnow and Sanger 1982, Sanger 1983, Sanger 1987b). The OCSEAP compilation (Sanger 1983) revealed a broader prey spectrum compared to systematic studies (Carter 1984, Sealy 1975c, Vermeer 1992), though this may have been partially because of the larger time period and larger geographic extent of collection (*table 1*). It may also have been a function of the larger sample size compared to these other studies (*table 1*).

Comparison of results from Sealy (1975c), Carter (1984), and Vermeer (1992) reveals the influence of site-specific conditions on prey availability and selection by murrelets (*table 1*). Differences between adult, nestling, and fledgling diet were also apparent (Carter 1984, Mahon and others 1992, Sealy 1975c) (*table 1*).

Though much work needs to be done on food habits in different geographic regions and seasons, in general it can be said that murrelets feed on invertebrates such as euphausiids, mysids, decapods and amphipods, and small schooling fishes including sand lance, anchovy, herring, smelt, and seaperch. The fish portion of the diet is most important in the summer and coincides with the nestling and fledgling period (Carter 1984, Carter and Sealy 1990, Sealy 1975c).

Prey Ecology

Because few systematic studies of murrelet food habits have taken place and the murrelet occupies such a large geographic area with a wide variety of fish species potentially available, the rest of this chapter will focus on selected prey species considered most important in murrelet diet at this time. Due to the long-standing commercial value of anchovies, herring, and sardines, there is a large body of information on life history and factors affecting their abundance and distribution. The following overview is not an attempt to compile the rich literature on these or the other known prey species, but instead focuses on interesting aspects of their life history and the interrelationship between prey species, murrelets, humans, and the marine environment. The relationship between other seabirds and these same prey resources, along with the marine environment, will be discussed. Sand lance and euphausiids have been little studied compared to the commercially valuable fish species, but are discussed first because of their position and interaction in the marine food web, and their importance in the murrelet's diet.

Euphausiids

Euphausiids are a group of small crustaceans which make up part of the zooplankton ("krill") found in the marine environment. Euphausiids are more or less transparent and phosphorescent and closely resemble shrimps in form though they are often not more than 25 mm long. The phosphorescent organs are along the sides of the body. Their purpose is not known. Attached to the thorax are the eight pairs of two-branched legs which give rise to the name "schizopoda," as this order was formerly called (Johnson and Snook 1967: 293-294).

Zooplankton are found in greater abundance during cold-water years in California waters. Many of the zooplankton are predators on fish eggs and larval fish, and their abundance was sometimes twenty times greater during the colder periods (Reid and others 1958). Accordingly, not only would the lowered temperature affect survival of fish eggs and larvae directly, it would also add to the hazards of being eaten by providing conditions for the rapid increase of zooplankton (Ricketts and Calvin 1962: 394).

Komaki (1967) summarized information obtained from fishermen on the phenomenon of surface swarming of euphausiids (*E. pacifica*) in the Sea of Japan. This phenomenon differs from the usual vertical migratory behavior because it occurs in the daytime, independent of light intensity. The swarming season in the Kinkazan waters ranged between late February and late May. Water temperature was determined to be the most important factor, with swarming starting at a slightly higher temperature than the local minimum (7 degrees Celsius), continuing with increasing temperature, and then terminating as the temperature exceeded 16 degrees Celsius. Because swarming did not occur earlier in the year when temperatures were favorable, Komaki (1967) concluded that the swarming was related to reproduction. Also, it appeared that the population was composed of several stocks, and that as stocks reached a certain degree of maturity, they approached the coast in succession.

The daily phenomenon of vertical migration was noted as early as 1872 during the Challenger Expedition. Many plankton animals actively move towards the surface of the ocean at night and sink or swim away to the depths in the daytime. Vertical climbing requires much energy and has been developed so frequently in the animal kingdom that it was thought to clearly be of some significance in the lives of such animals (Hardy 1965: 199–200). The main proximate factor for daily vertical migration appears to be light intensity (Cushing *in* Raymont 1963: 435).

Both *E. pacifica* and *T. spinifera* were found to undergo vertical migration off Washington State in summer 1967 (Alton and Blackburn 1972). High catch rates were sustained from near-surface water throughout the late evening and early morning hours, approximately 2200 to 0500 hours.

Hardy (1965: 212–215) advanced a general theory for the value of diurnal vertical migration. Because the uppermost layers of the sea generally move at higher speeds than lower levels and bottom topography results in currents which may differ from surface layers, the regular movement of plankton between these layers allows the animals to be carried over greater distances than would otherwise be the case. Thus, the plankton population can be distributed over a much larger area of the ocean than if continually moved by only one body of water. This large-scale movement has the advantage of putting the animals in contact with more food source patches. Individual variation in the degree of vertical migration and the amount of time spent at any one layer further promote the patchy distribution of plankton.

A genetic theory has also been proposed (David *in* Raymont 1963: 466). Marine planktonic species may tend to become divided into relatively small, separate populations if continually drifting in one stratum and not normally encountering directional stimuli to encourage horizontal migration. However, the broader distribution caused by vertical migration would help to encourage interchange of zooplankton populations and thus promote gene flow.

There are many other theories regarding vertical migration. The fact that both Raymont (1963) and Hardy (1965) devoted an entire chapter to the subject attests to the complexity of factors which operate in the marine environment. As summarized by Hardy (1965: 217): "There can be no doubt that the patchy distribution of the plankton must be due to a great variety of causes." Raymont (1963: 466) ended his chapter by recognizing the need for more research on the subject: "At this stage no conclusive answer can be given to the question as to the value of diurnal vertical migration, but the tremendously wide occurrence of this phenomenon in the seas is one of the most challenging aspects of marine plankton study."

With the variability in zooplankton distribution and abundance, the way in which murrelets find such prey resources warrants attention. The interannual variability in euphausiid consumption (*tables 2* and *3*) noted by Krasnow and Sanger (1982) could demonstrate differences in zooplankton distribution (rather than abundance) and the corresponding inability of murrelets to locate and use the resource. However, some of the distribution patterns should be predictable at least between "normal" years, and thus the learning of foraging areas by murrelets would indeed be important for minimizing energy expenditure as suggested by Carter (1984). Komaki (1967) demonstrated that *E. pacifica* and sand eels (*A. personatus*) fluctuated in parallel on the basis of data on fishery harvest, and that sand eels were taken in almost the same area as the euphausiid fishery. The traditional euphausiid swarming areas were known to the fishermen, though the density of the swarm varied between years (Komaki 1967). Thus, conservation of the murrelet and its food web will be aided by identification and appropriate management of important euphausiid swarming areas, especially in the vicinity of known murrelet nesting areas.

Pacific Sand Lance

Sand lance are slim, elongated, usually silver fishes especially abundant in northern seas. They belong to the ammodytidae and are sometimes called sand eels, but they are not true eels even though eel-like in shape and movement. The Pacific sand lance is distributed from southern California to Alaska and to the Sea of Japan.

They grow to about 20 centimeters in length (Miller and Lea 1972). There has been much confusion over the taxonomy of the sand lances throughout the world since they are similar in external appearance (Hardy 1965: 209–210; McGurk and Warburton 1992). Of this confusion Hardy (1965: 210) wrote, "It all goes to show how elusive...these sand-eels are. They are all very much alike; little silvery eel-like fish which occur in large shoals in sandy parts of the sea and escape from their predators by diving like a flash into the sand and becoming completely covered." They are most abundant in the shallow regions around the coast, but may also be found on sand banks far out on the continental shelf (Hardy 1965: 211).

The most interesting characteristic of the sand lances is their ability to burrow into sand or gravel and remain there for long periods. Both burrowing and emergence are extremely rapid, the fish entering and leaving the surface almost vertically at swimming speed. Coastal sand lance may bury themselves above low-water mark and remain buried as the tide recedes and until it covers the area again. This habit demands a loose, porous substrate in which respiratory water maintains sufficient oxygen to support life (Scott 1973).

Food habits of 486 specimens (15-31 cm) of northern sand lance (*A. dubius*) taken at various localities and seasons from Nova Scotia Banks revealed copepods as the most frequent food item, followed by crustacean larvae, invertebrate eggs, and polychaete larvae. Volumetric analysis showed copepods to comprise the bulk of the food (65 percent), followed by polychaete larvae (15 percent) and euphausiids (14 percent). The latter two food items were selected for in greater volume when compared to availability, since euphausiids made up less than 4 percent of the volume of simultaneous plankton tows (Scott 1973).

McGurk and Warburton (1992) conducted an intensive study of environmental conditions and the effects on sand lance larvae in the Port Moller estuary in Alaska. They found that three waves of spawning sand lance entered the estuary from mid-January to late May. Peak spawning occurred in January, March, and April. Eggs incubated for a period of 45 to 94 days. Slow growth was directly responsible for the reduced number of cohorts and the long time periods between peak hatch dates compared to other demersally-spawning fish such as herring or capelin, because first-feeding sand lance larvae took longer to vacate their feeding niches. The larvae fed primarily during the day on a diet of copepod eggs and nauplii, copepodites, and small adult copepods. This type of prey and its average length and width were similar to that of herring larvae, indicating that the larvae of these two species shared the same food resource.

McGurk and Warburton (1992) concluded that the stock of sand lance that spawns in Port Moller belongs to a class of stocks that have an entirely estuarine or coastal early life history, in contrast to some stocks of sand lance whose larvae disperse offshore from inshore spawning sites. This life history strategy may have evolved in response to the unique physical conditions of the Port Moller estuary—a shallow, well-mixed site with sandy substrate that is suitable for incubation of demersal eggs next to a deep, stable fjord with a rich zooplankton community that is suitable for rearing of larval and juvenile sand lance.

Variation in physical factors, particularly, storm events, local wind-forced surface currents, baroclinic surface currents, and regional downwelling events at the boundary of the estuary cause annual variation in recruitment. Additionally, density-dependent factors such as competition for food between sand lance, between sand lance and other planktivorous fish larvae such as herring, and between sand lance and invertebrate planktivores such as chaetognaths may play as important a role as density-independent physical factors (McGurk and Warburton 1992). McGurk and Warburton noted that the small scale of dispersal in the Port Moller stock also leaves it more vulnerable to industrial development such as dredging or release of toxic chemicals.

Sherman and others (1981) summarized research in the North Sea which documented an increase in sand eel (*Ammodytes* sp.) as a result of depleted herring and mackerel (*Scomber* sp.) stocks. In the absence of a sand lance fishery on the east coast of North America from which to estimate population trends, researchers in this area used ichthyoplankton surveys. As in the North Sea, population explosions of small, fast-growing sand eel coincided with depletions of larger tertiary predators, including herring and mackerel. From 1974 to 1979 the percentage of sand eel increased from less than 50 percent of the total mid-winter ichthyoplankton community to more than 85 percent (Sherman and others 1981). This change followed significant fishing stress of the northwest Atlantic ecosystem, where fish biomass in the region was reduced by 50 percent from 1968 to 1975 (Clark and Brown *in* Sherman and others 1981).

Clark and Brown concluded that reductions in herring and mackerel on both sides of the Atlantic in response to heavy fishing mortality, followed by increases in sand eel and other small, fast-growing fish, made unlikely the hypothesis that the changes were due to environmental factors. They concluded that, when a large biomass of mid-size predators is removed, it can be replaced by smaller, faster-growing, opportunistic species (Sherman and others 1981).

This relationship was further evaluated by Fogarty and others (1991) with a mathematical model. A significant negative interaction between sand lance recruitment and an integrated measure of herring and mackerel biomass was indicated. However, since both herring and mackerel feed on sand lance, it was impossible to distinguish the relative roles of the two predators. The authors concluded that direct evidence of predation by mackerel and herring was available to support the inference of interactions between sand lance and pelagic predators, though alternative hypotheses could be formulated.

Recent changes in the population of sand eels (*Ammodytes marinus*) at Shetland were studied in relation to estimates of seabird predation (Bailey and others 1991). Since 1974 there has been a sand eel fishery in inshore waters around Shetland,

and landings have decreased. Simultaneously, there was a decrease in consumption of sand eels by seabirds. These findings indicate that the switching of seabirds from sand eels to other prey is in approximate proportion to the abundance of sand eels. However, Bailey and others (1991) concluded that more data were needed to significantly refine the analysis. It was noted that different seabirds respond differently to changes in stock. Surface feeders must forage close to the colony and make many fishing trips per day; thus they are especially sensitive to reduction in food availability. This is in agreement with evidence that Arctic Terns (*Sterna paradisaea*) showed the earliest and most severe breeding failures at Shetland (Heubeck *in* Bailey and others 1991). By contrast, some of the larger seabirds with generalist feeding abilities took sand eels when these were abundantly available but switched diet as the sand eel stock declined.

The relationship between British [Black-legged] Kittiwake breeding success and the Shetland stock of sand eels (*Ammodytes*) was studied by Harris and Wanless (1990). The evidence that food shortage was responsible for low breeding success was mostly circumstantial but, taken as a whole, compelling. However, the authors concluded that natural factors could have caused the decline in the sand eels, rather than overfishing (Kunzlik *in* Harris and Wanless 1990). They also suggested that herring predation was responsible for the fishery decline. As in the other studies of seabirds and sand lance described above, the authors concluded that more comprehensive studies were needed to allow definitive interpretation of the results.

More studies on the Pacific sand lance are needed on the west coast of North America, especially on environmental effects and predator influence on survival and abundance. Spawning areas of sand lance need to be identified and managed. The trophic links between sand lance and two other murrelet prey items, euphausiids and herring, indicate a need for comprehensive, long-term study and management.

Northern Anchovy

These fish belong to the engraulidae family. They have no adipose fin or lateral line and are closely related to herring.

The following life history information (for anchovies and sardines) was taken from a draft document (Anonymous 1993) which was not completed or published because of a change in Pacific coastal pelagic species management policy between regulatory agencies (Wolf, pers. comm.).

Northern anchovy are distributed from the Queen Charlotte Islands, British Columbia, to Magdalena Bay, Baja California. The population is divided into northern, central, and southern subpopulations, or stocks. The central subpopulation, which supports significant commercial fisheries in the United States and Mexico, ranges from approximately San Francisco, California, to Punta Baja, Baja California. The northern subpopulation supports a small but locally important bait fishery in Oregon and California.

Anchovies are small, short-lived fish typically found in schools near the surface. The fish rarely exceed 4 years of age and 18 cm in total length. They have a high natural mortality; approximately 45 to 55 percent of the total stock may die each year of natural causes in the absence of fishing. Northern anchovy eat plankton either directly or by filter feeding.

Anchovy spawn during every month of the year, but spawning increases in late winter and early spring and peaks from February to April. The eggs, found near the surface, are typically ovoid and translucent and require two to four days to hatch, depending on water temperature. Anchovy are all sexually mature at age 2. The fraction of one-year-olds that is sexually mature in a given year depends on water temperature and has been observed to range from 47 to 100 percent (Methot *in* Anonymous 1993).

Northern anchovy in the central subpopulation are harvested by commercial fisheries in California and Mexico for reduction, human consumption, live bait, dead bait, and other nonreduction commercial uses. Anchovy landed in Mexico are used primarily for reduction although small amounts are probably used as bait. Small quantities of the northern subpopulation are taken off Oregon and Washington for use as dead bait.

Anchovy landed by the reduction fisheries are converted to meal, oil, and soluble protein products sold mainly as protein supplements for poultry food and also as feed for pigs, farmed fish, fur-producing animals, laboratory animals, and household pets. Meal obtained from anchovy is about 65 percent protein.

Anderson and others (1980) compared estimates of anchovy biomass and catch statistics to Brown Pelican (*Pelecanus occidentalis californicus*) reproductive success. Brown Pelican diet was composed of 92 percent anchovies in the Southern California Bight (SCB) study area. Mean SCB anchovy biomass (square miles of anchovy schools) and mean pelican reproductive rate (number of fledglings per nesting attempt) were highly correlated. It was estimated that a minimum anchovy biomass of 43 square miles was necessary for maintaining the existing pelican reproductive rate, though it was recognized that the rate would have to increase in order to at least maintain the pelicans in the SCB. Secondly, the minimum biomass estimate was almost twice the forage reserve which was recommended at the time in the Anchovy Management Plan. They regarded the information as preliminary and concluded that better estimates of the forage reserve were needed.

A similar relationship between anchovies and Elegant Terns (*Sterna elegans*) was described by Schaffner (1986). Breeding pairs of Elegant Terns and estimates of anchovy spawning biomass were significantly correlated for the period of 1979 through 1983. Additionally, extensive overlap in age compositions of the tern and fishery samples suggested they were using similar resources and the potential for competition existed. Anchovies constituted more than 86 percent of the chick regurgitations when population size peaked. Schaffner (1986) pointed out the similarities to the Brown Pelican study and advised that a close watch of the situation was in order because of declining anchovy populations.

Anderson and others (1980) proposed the establishment of protected foraging zones as critical habitat under the federal Endangered Species Act in order to assure adequate pelican reproduction and conservation. However, they recognized that because of the unpredictable nature of anchovy distribution, such areas could be difficult to define between seasons and between years. Protection of marine habitat as critical habitat for the murrelet has also been recommended by researchers, the Marbled Murrelet Recovery Team, and the California Department of Fish and Game.

Pacific Sardine

These small pelagic clupeids occur in the California Current system from southern Baja California to southeastern Alaska, and in the Gulf of California. In the northern portion of the range, occurrence is seasonal. It has been generally accepted that the sardine population off the west coast of North America consists of three subpopulations. A northern subpopulation (northern Baja California to Alaska), a southern subpopulation (off Baja California), and a Gulf of California subpopulation were distinguished on the basis of serological techniques (Vrooman *in* Anonymous 1993).

Historically, the sardines migrated extensively, moving north as far as British Columbia in the summer and returning to southern California and northern Baja California in the fall. The migration was complex, and timing and extent of movement were affected to some degree by oceanographic conditions (Hart *in* Anonymous 1993).

Sardines reach about 41 cm in length, but usually are shorter than 30 cm. They live as long as 13 years, although most sardines in the historical and current commercial catch are 5 years and younger. They spawn in loosely aggregated schools in the upper 50 meters of the water column probably year-round, with peaks from April to August. Spawning has been observed off Oregon, and young fish have been seen in waters off British Columbia, but these were probably sporadic occurrences (Ahlstrom *in* Anonymous 1993). The spatial and seasonal distribution of spawning is influenced by temperature.

Sardines prey on crustaceans, mostly copepods, and consume other phytoplankton, including fish larvae. Larval sardines feed extensively on the eggs, larvae, and juvenile stages of copepods, as well as on other phytoplankton and zooplankton.

The fishery began in central California in the late 1800's and developed in response to a demand for food during World War I (Schaefer and others *in* Wolf 1992). The Pacific sardine supported the largest fishery in the Western Hemisphere during the 1930's and 1940's, with landings in British Columbia, Washington, Oregon, California, and Mexico. The fishery declined, beginning in the late 1940's and with some short-term reversals, to extremely low levels in the 1970's. There was a southward shift as the fishery decreased, with landings ceasing in the northwest in 1947-1948, and in San Francisco in 1951-1952. The regulatory history of the sardine fishery might best be described as "too little too late." Regulatory authority for the sardine fishery in California rested with the legislature, which delegated only limited authority to the Fish and Game Commission. State biologists had expressed concern about the size of the fishery as early as 1930. Industry opposed any regulation of total catch, and an intense debate began over whether the decline of the sardine fishery and population was due to overfishing or environmental factors (Clark and Marr *in* Wolf 1992).

It was not until 1967, well after the fishery had collapsed, that the California legislature passed an "emergency" bill declaring a 2-year moratorium on fishing sardines, and in 1974 another bill was enacted which established a complete moratorium on directed fishing for sardines, though an incidental catch provision continued. A small directed fishery was first allowed in 1986 and the directed quota has recently been enlarged (Wolf 1992).

Since the early 1980's, sardines have been taken incidentally with Pacific (*Scomber japonicus*) and jack mackerel (*Trachurus symmetricus*) in the southern California mackerel fishery and primarily canned for pet food, although some were canned for human consumption. Sardines landed in the directed sardine fisheries off California are primarily canned for human consumption and sold overseas.

Management of the sardine is difficult in the absence of a large fishery since a precise, direct estimate of a relatively small biomass is difficult and expensive to obtain (Wolf 1992). Integrated methods of stock assessment will be necessary to manage this resource (Barnes and others 1992).

Baumgartner and others (1992) presented a composite time series of anchovy and Pacific sardine fish-scale-deposition rates which they developed from sampling the anaerobic layered sediments of the Santa Barbara Basin off southern California. Other researchers (Soutar; and Soutar and Isaacs *in* Baumgartner and others 1992) had previously collected information on the deposition rates of these species, but their sample sizes were limited and there was uncertainty in the underlying chronology because of imperfect preservation of the annually deposited layers. The new sardine and anchovy series provide significantly more reliable estimates of the scale-deposition rates (SDR's) (Baumgartner and others 1992). An overriding lesson from the Santa Barbara records is that in the past both sardines and anchovies experienced large natural fluctuations which were clearly unrelated to fishing, and that abrupt natural declines, similar to the collapse of the sardines during the 1940's, are not uncommon.

The scale-deposition record shows nine major recoveries and subsequent collapses of the sardine population over the past 1,700 years. The average time for a recovery of the sardine is 30 years. Sardines and anchovies both tend to vary over a period of approximately 60 years. In addition, the anchovies fluctuate at a period of 100 years. There is a moderate correlation between sardines and anchovies over long time scales of several centuries or more, but the correlation of shorter-period components in the time series is virtually nil.

Baumgartner and co-authors say that caution in interpreting the data should be exercised on two fronts: (1) sample size; they acknowledge that additional samples are needed to capture the complete range of variability of the SDR's over the basin. (2) The collapse and recovery demonstrated for the sardine do not necessarily mean that the current cycle of collapse and recovery has no relation to the application/release of fishing pressure or change in ocean climate, or both. They infer that even though the causes may vary (biological interaction, environmental change) for different recoveries or collapses, the sustained reproductive consequences are similar from one event to another (Baumgartner and others 1992).

Analysis of fish scales in sediments of the central Gulf of California resulted in similarities with the Santa Barbara Basin work (Holmgren-Urba and Baumgartner 1993). The reconstructions show a strong negative association between the presence of sardines and anchovies, with anchovies dominating throughout the 19th century, and with only two important peaks of sardine scale deposition. The two episodes of sardine scale deposition occur virtually 180 degrees out of phase with anchovy scale deposition. This suggests an overall coherent pattern in changing ecosystem structure that operates over a period of about 120 to 140 years. The collapse of the sardine population in the Gulf of California was very similar to the collapse in the California Current during the late 1940's and 1950's. Both populations declined under heavy fishing pressure (Barnes and others 1992) superimposed on broad, natural, decadal-to-centennial-scale biomass fluctuations (Soutar and Isaacs *in* Holmgren-Urba and Baumgartner 1993). Both declines appear to be accompanied by an increasing population of northern anchovy (MacCall and Praeger *in* Holmgren-Urba and Baumgartner 1993). The relationship to climate was not entirely clear, but suggested a mediating effect on population sizes. However, the process is still subject to strong filtering through biological interaction among species.

Butler and others (1993) modeled anchovy and sardine populations to examine how natural variation of life-history parameters affected per capita growth. The greatest change in growth for both species occurred during larval stages. A number of important life history parameters of marine fish are directly affected by changes in temperature, and temperature and food densities affect growth at all stages. For anchovies, there is some evidence that reproduction is drastically reduced during major El Niño events. Under such conditions, the anchovy stock declined. For the sardine, high fishing mortality reduces the abundance of the oldest age classes, which have the highest reproductive potential because of their larger size and greater number of spawnings. Density-dependent factors such as cannibalism on eggs may also be important (Valdes and others and Valdes Szeinfeld *in* Butler and others 1993). The results of this modeling exercise parallel the results and conclusions of McGurk and Warburton (1992) described earlier in the section under sand lance.

Structural changes over time in the California Current ecosystem between sardines and anchovies are similar to changes between herring and sand lance described previously for the North Sea and the Atlantic, though different factors were probably operative. Additionally, most researchers have found it difficult to separate the effects of humans from natural influences on the fish stocks. The fact that both mechanisms will continue to operate dictates that managers conduct effective monitoring programs and adaptive management to allow prompt remedial action to be taken where necessary (Wilson and others 1991).

The low occurrence of sardines in the diet of murrelets is interesting given the wide geographic distribution of this fish (*table 1*). This low occurrence may be due to fewer studies in the southern end of the murrelet's geographic range where sardines are more abundant. Alternatively, it may represent an overall lower abundance due to overfishing, competition, and natural influences. Anderson and Anderson *in* Anderson and others (1980) suggested that past breeding populations of Brown Pelicans in the Southern California Bight probably had a larger prey base than the existing anchovy-dominated diet, perhaps also importantly involving Pacific sardines and Pacific mackerel. Recent increased abundance of sardines off southern California was followed by increased breeding success and abundance of Brown Pelicans (Ainley and Hunt *in* Anonymous 1993).

Because of the natural fluctuations in anchovies and sardines as shown from the scale-deposition studies, murrelets probably evolved to use this resource in proportion to availability. Thus, the periodic lows in anchovy and sardine populations would probably not adversely affect the murrelet as long as alternative forage fish remained available. Development of new fisheries (sand lance or euphausiids) and escalation of harvests for rockfish and herring would be expected to affect murrelets, especially in conjunction with a low period of anchovies and sardines, and El Niño events.

Pacific Herring

Herring belong to the clupeidae as do the Pacific sardine. Adults range up to 45 cm in length (Miller and Lea 1972: 54). Herring are one of the most abundant species of fishes in the world and prey upon copepods, pteropods, and other planktonic crustaceans, as well as fish larvae. They travel in vast schools, providing food for larger predators.

The Pacific herring ranges from Baja California to Alaska and across the north Pacific to Japan. Within this range, abundance generally increases with latitude and the largest populations are centered off Canada and Alaska (Spratt 1981).

Currently, all herring commercially harvested in California and Oregon are taken as sac-row for Japanese markets. In British Columbia and Alaska, herring are primarily harvested for sac-row, and as longline bait (McAllister, pers. comm.).

Spawning begins during November in California and ends during June in Alaska, becoming progressively later from south to north. During the spawning season, herring congregate in dense schools and migrate inshore where they deposit their sticky eggs on vegetation found in intertidal and shallow subtidal areas of bays and estuaries. The eggs hatch in about 2 weeks. After spawning, herring return to the open ocean where their movements are largely unknown (Spratt 1981). The large herring fisheries are subject to great fluctuations in their annual catches because the survival of young herrings varies widely from year to year, with a heavy dependence on copepods (Hardy 1965: 62). The fish mature in about 4 years and may live 20 years.

Information on the age structure of spawning herring was analyzed by Lambert (1987). He noted that it is an underappreciated fact that herring often arrive at spawning grounds in runs or waves. This phenomenon has been reported in both the Atlantic and Pacific Oceans for *C.h. harengus* and *C.h. palasii*. It is suggested that spawning proceeds consecutively through year classes from oldest to youngest due to differential maturation. Discrete batches of eggs deposited by these waves of spawning herring give rise to a succession of larval cohorts. The more age classes involved in spawning, the longer will be the spawning season and the spawning will be more widespread since different age groups tend to spawn in different areas. Therefore, it would appear that the maintenance of a wide, well-balanced age structure tends to promote a resilient or more stable population (Lambert 1987).

Near the Queen Charlotte Islands in British Columbia, shoals of immature herring occur frequently at the surface, where they often jump clear, making a calm sea suddenly erupt in a tiny “boil.” Herring boils are often associated with swarms of euphausiids which provide food for the herrings (Gaston 1992: 74). Many seabird species will be found feeding at such prey concentrations.

In his chapter on the herring, Hardy (1965: 61) wrote: “Early in the year, in March and April, the North Sea herring is feeding very largely on young sand-eels [*Ammodytes* sp.]; and often at this season you will find the stomach of the herring crammed full of them, lying neatly side by side like sardines in a tin.”

McGurk and Warburton (1992) found that herring and sand lance larvae consumed prey of similar lengths and widths. They concluded that herring and sand lance larvae compete for substantially the same prey resource. More than 99 percent of the prey items found in the guts of sand lance larvae were various life history stages of copepods (McGurk and Warburton 1992).

The work of Carter (1984) and Vermeer (1992) indicated the importance of herring in the diet of murrelets (*table 1*). Lid (1981) suggested that the breeding failure of Puffins [Atlantic Puffins] (*Fratercula arctica*) in Norway was due to over-harvesting of herring and, to some extent, over-fishing of sand eels (*Ammodytes* sp.). Many puffin chicks died, and adult weights were lower during the study period. Spawning stock size in weight of the Norwegian spring-spawning herring declined from approximately 9.5 million tons to less than 0.5 million tons between 1950 and 1980 (Lid 1981).

Commercial fishing harvest of herring should be monitored for effects on murrelet reproductive success. In the absence of a sand lance fishery on the west coast of North America, it may be that sand lance populations will respond positively to reduction in herring as documented elsewhere. However, murrelet use of either of these resources will depend on temporal and spatial distribution of the prey relative to murrelet nesting and foraging habitat. The patchy distribution of prey during different seasons must be considered along with changes in offshore distribution of the murrelet between seasons.

Smelt

The osmeridae are closely related to salmon and trout, and like trout, have a small, adipose fin. They are confined to arctic and north temperate waters and are best represented in the north Pacific basin. All spawn in fresh water or along the seashore (Hart and McHugh 1944). Among related Pacific species are the surf smelt or silver smelt (*Hypomesus pretiosus*), capelin, and eulachon or candlefish.

The silversides (atherinidae) and other unrelated fishes are sometimes also called smelts, sand smelt, or whitebait. The atherinidae also include grunion (*Leuresthes tenuis*) which occurs north only to the San Francisco area.

The eulachon has been called candlefish because the flesh is so oily that the dried fish, when provided with a wick of rush-pith or strip from the inner bark of cedar, burns with a steady flame and was used as a candle by the natives. This fish gave rise to the famous “grease trails” which roughly follow the courses of the great northern rivers (Hart and McHugh 1944). The only record of eulachon in murrelet diet was the anecdote by Grinnell (1897) described previously under the section on Alaska. Eulachon are distributed from northern California to the Bering Sea. They seem to feed primarily on euphausiids. Eulachon are important as an intermediate step in the food chain between the euphausiids and larger fish (Hart and McHugh 1944).

The range of the silver smelt extends from southern Alaska to central California. Some of the smelt may spawn at the end of the first year as has been indicated for Puget Sound fish. They spawn under a great variety of conditions and in most months of the year. Summer spawnings take place both on exposed beaches and at the head of sheltered bays. Usually the fish spawn where there is a certain amount of seepage of fresh water through the fine gravel to which the eggs adhere. Euphausiids seem to be the main food item consumed by silver smelt (Hart and McHugh 1944).

The capelin is an arctic species with its center of abundance in the Bering Sea or Arctic Ocean (Hart and McHugh 1944). In the Pacific, capelin occur from Alaska to Juan de Fuca Strait. Their distribution in the coastal zone varies seasonally but peaks in June and July when beach spawning occurs. At other times of the year, capelin can be found in large concentrations in the offshore waters (Jangaard *in* Carscadden 1984). At spawning time, capelin appear in schools of considerable size along the shores of gravelly beaches. Spawning occurs in the evening at high tide right at the water's edge. Studies of the beach both during and after spawning indicate that a specific type of ground is selected, the fish tending to avoid both rocky and sandy patches. The eggs are extremely adhesive and immediately become firmly cemented to the gravel (Hart and McHugh 1944).

Capelin mature at 3 or 4 years of age with faster growing fish maturing earlier (Winters *in* Carscadden 1984). In the spawning populations, 3- and 4-year-olds usually predominate. Spawning mortality is high, usually greater than 80 percent (Carscadden and Miller *in* Carscadden 1984).

Like other pelagic fish species, capelin populations exhibit large variations in abundance of year classes, and natural fluctuations in abundance are often complicated by the presence of fishing mortality. Carscadden (1984) evaluated fluctuations in capelin biomass in the northwest Atlantic and concluded they were the result of natural variation in year-class strength. The causes of the variation were not well understood, but temperature and onshore wind-induced wave action have been correlated with emergence of larval capelin (Frank and Leggett *in* Carscadden 1984).

Carscadden (1984) considered the relationship between Atlantic Puffins and capelin as described by Brown and Nettleship (1984) and concluded that a complex of natural environmental and biological factors would probably affect the abundance and behavior of capelin predators, rather than a single one such as abundance of capelin. Brown and Nettleship (1984) concluded that the management of the capelin fishery in the northwest Atlantic should "proceed cautiously" until the relationships between the capelin and its predators were better understood.

Vader and others (1990) evaluated the relationship between Common Murres, Thick-billed Murres (*U. lomvia*), and capelin in Norway. A complete collapse of the Barents Sea stock of capelin occurred between 1985 and 1987, and in 1987 fishermen noted a near-complete absence of sand lance. The low sand lance population resulted in a complete breeding failure of Shags (*Phalacrocorax aristotelis*) in West Finnmark, where Shags are normally totally dependent on sand lance during the breeding season. A sudden drop in breeding Common Murres also occurred in 1987. The authors concluded that the capelin and sand lance food shortage caused the large drop in Common Murres and the reduced breeding of Thick-billed Murres. The authors thought the larger prey spectrum utilized by the Thick-billed Murres allowed that population to fare better than the Common Murres in the face of the food shortage. The causes of the decline in capelins probably included overfishing, uncommonly large year-classes of the predatory cod (*Gadus morhua*), and a reduction in recruitment due to changes in the physical oceanography of the Barents Sea (Hamre; Ushakov and Ozhigin *in* Vader and others 1990).

The importance of capelin in the diet of the murrelet in the Gulf of Alaska (Sanger 1983) indicates the need to monitor and manage carefully this resource. Other smelt species may be important in murrelet diet; unidentified osmerids have been documented as murrelet prey over a broad geographic range (*table 1*). Further research is needed on the importance of smelt in the diet of the murrelet, especially in Washington, Oregon, and California.

Prey Ecology Summary

The marine environment, especially in an eastern boundary current system, is not static (Ainley and Boekelheide 1990: 376). In his book on the Ancient Murrelet, Gaston (1992: 74) wrote of a diagram of the food web of Reef Island: "A complete diagram of the food webs of Hecate Strait would probably cover a baseball field at this scale, and would take several lifetimes of research to construct." Sanger's (1983) compilation contains numerous food web diagrams which depict the complex interactions in the marine environment. A food web and a model of the trophic-level interactions influencing murrelets at any site in North America would be complex indeed, but much information on life history of prey species and the murrelet at sea must be gathered.

From the studies discussed above, some variability in reproductive success of the murrelet can be expected because of the naturally dynamic nature of their prey base and the marine environment. Anthropogenic influences can compound prey fluctuations; thus, marine research and management should be designed to minimize or avoid adverse changes in seabird reproduction and marine trophic-level interactions. Anthropogenic and environmental influences will continue to affect marine ecosystems. Management must therefore entail monitoring and the ability to change course in response to observed effects. Cumulative impacts in localized areas of murrelet abundance should be anticipated and averted.

Size of Prey Items

A compilation of prey item size in the diet of adult and subadult murrelets from systematic studies indicates the majority of fish taken ranged from 30.1 to 60.0 mm (*table 4*). The largest combined sample size was for sand lance, and the distribution indicated a heavy reliance on fish up to 60.0 mm, although fish greater than 90.0 mm were also taken. Sanger (1987b) calculated a mean value of 45 mm (total length) for sand lance which correlates well with the distribution of prey size revealed in *table 4*. Smaller size classes (0.1-30.0 mm) of scorpaenids and *Cymatogaster aggregata* were taken by murrelets; this could be a function of availability or preference. Larval and juvenile fish (0.1-60.0 mm) appear to be the main size classes eaten by adult and subadult murrelets. Larval fish are underrepresented in murrelet diet because they are digested quickly (Carter 1984), therefore, the overall importance of larval fish for murrelets is difficult to assess.

The size of prey items in the diet of hatching-year and nestling murrelets is markedly different (*table 5*) though a comparison of fish lengths in *tables 4* and *5* reveals adult/subadult and hatching-year murrelet prey size to be similar.

Table 4—Size of prey items for adult and subadult Marbled Murrelets

Prey	Sample size *n*	Mean length *mm*	Range or size class *mm*
Loligo opalescens	5[a]	–	0.1–30.0
	2[b]	–	>24.0
Unidentified mysids	20[c]	18	11–38
Unidentified gammarid amphipod	6[c]	15	12–18
Thysanoessa inermis	2[c]	–	15–21
Thysanoessa raschii	38[c]	14	11–21
Thysanoessa spp.	24[c]	13	11–18
Thysanoessa spinifera	1[c]	24	–
	21[b]	–	0.1–12.0
	149[b]	–	12.1–24.0
	237[b]	–	>24.0
Euphausia pacifica	34[b]	–	12.1–24.0
Clupea harengus	35[a]	–	0.1–30.0
	101[a]	–	30.1–60.0
	26[a]	–	60.1–90.0
Engraulis mordax	4[a]	–	30.1–60.0
Mallotus villosus	18[c]	63	28–105
Osmeridae	6[b]	–	0.1–30.0
	11[b]	–	30.1–60.0
Scorpaenidae	29[b]	–	0.1–30.0
	3[a]	–	30.1–60.0
Cymatogaster aggregata	32[b]	–	0.1–30.0
	14[b]	–	30.1–60.0
	1[b]	–	60.1–90.0
Stichaeidae	6[b]	–	30.1–60.0
Ammodytes hexapterus	13[c]	45	29–135
	528[ab]	–	0.1–30.0
	596[ab]	–	30.1–60.0
	88[ab]	–	60.1–90.0
	6[b]	–	>90.0

[a] Carter (1984); length for invertebrates is total length, and fork length for fish

[b] Sealy (1975c); length same as Carter (1984) except as noted for *Loligo opalescens*

[c] Sanger (1987); length for all specimens is total length

As noted by Carter (1984) and Mahon and others (1992), murrelet nestlings are fed much larger fish than the adults consume. Most nestling prey items were >60.1 mm, and sand lance prey were >90.1 mm (*table 5*).

Schweiger and Hourston *in* Carter (1984) concluded that second-year herring fed to nestlings were much less abundant than the juvenile herring that adult murrelets ate for themselves. Second-year sand lance and anchovy were also not considered very abundant in Carter's (1984) study area, which suggested that murrelets selected larger prey to carry to nestlings, even though such fish were less abundant. This behavior is consistent with optimal foraging theory (Carter and Sealy 1990), and other seabirds have exhibited this same adaptive trait (Gaston and Nettleship; and Slater and Slater *in* Carter 1984).

The lengths of nestling prey probably represent second-year fish (Hart *in* Carter 1984), thus, murrelet adults, subadults, and hatching-year birds feed primarily on larval and juvenile fish, whereas nestlings are most commonly fed second-year fish. Therefore, both of these cohorts of the principal prey species should be monitored and managed to assure maximum productivity of murrelets in any one year.

Energetics and Energy Values of Some Prey Items

Energy values of prey items also help explain why murrelets select certain prey species for themselves and their

Table 5—Size of prey items for hatching–year and nestling Marbled Murrelets

Prey	Hatching-year prey size		Nestling prey size	
	Sample size	Range	Sample size	Length of specimen or range
	n	*mm*	*n*	*mm*
Clupea harengus	3[a]	0.1–30.0	16[a]	60.1–120.0[b]
	38[a]	30.1–60.0		
	7[a]	60.1–90.0		
Engraulis mordax	–	–	2[a]	90.1–120.0[b]
			1[c]	113
Mallotus villosus	–	–	1[d]	80
Ammodytes hexapterus	2[e]	0.1–30.0		
	25[ae]	30.1–60.0		
	2[e]	60.1–90.0		
			70[a]	90.1–120.0[b]
			Unknown[f]	140–180[b]
Cymatogaster aggregata	12[e]	0.1–30.0	–	–
Scorpaenidae	1[a]	30.1–60.0	–	–
Unidentified fish	–	–	56[a]	60.1–120.0[b]

[a] Carter (1984); 16 June - 6 July 1980, n = 144 fish observed.

[b] Sizes of prey estimated while held by murrelets in their bills when on the water

[c] Ralph and others (1990); observation during mist-netting operation, 3 July 1989.

[d] Simons (1980); observation of a feeding at a ground nest.

[e] Sealy (1975c); from 6 newly-fledged murrelets collected between 10 July and 4 August 1971.

[f] Mahon and others (1992); murrelets observed on the water in the evenings, 6 June - 8 August 1991.

nestlings. Energy values of seabird prey items have been little studied (Hislop and others 1991), but a gross comparison from some closely related species reveals marked differences in food energy, protein, and total lipids (*table 6*). Especially when considering the feeding of nestlings at inland sites, optimal foraging theory would predict that the largest and most energy-rich food items would be brought to the nestlings. This would be adaptive by reducing energy demand on the adults, and by increasing the chances of a successful fledging. However, prey availability and competition with other seabirds also affects prey selection. The small size of the murrelet also limits its prey load, and a long flight time inland with a heavy prey load would be energetically costly and would subject the bird to an increased period of vulnerability to inland predation. Prey also loses water during transport by seabirds. Montevecchi and Piatt *in* Hislop and others (1991) simulated transport of capelin by tying fish to a drying rack mounted on a pick-up truck which was driven at 60 km/h. After one hour, weight loss averaged 9 percent for male capelin and 11.5 percent for females.

A detailed analysis of variation in the calorific value and total energy content of the lesser sand eel (*A. marinus*) and other fish preyed on by seabirds was conducted in north Scottish waters by Hislop and others (1991). They found the calorific values and body weights of sand eels larger than 10 cm showed marked seasonal trends, and thus the total energy content of a sand eel of given length in summer was approximately double the spring value. Calorific values of Atlantic herring also varied from month to month, but seasonal cycles were less obvious. Seasonal cycles in fat content and, consequently, in calorific value are generally associated with the annual reproductive and feeding cycles of the fish, and tend to be greater among the larger, mature members of the population. Since different species of fish spawn at different times, their condition cycles are out of phase to some extent. And, since herring spawn in different waves, their condition is not uniform at any one point in time.

Hislop and others (1991) concluded that because fish demonstrate intraspecific length-related and seasonal changes in calorific value and energy content, it is unwise to generalize about the relative food values of different prey species to predators. They noted that sand eels have maximum calorific values intermediate between those of gadoids and clupeoids. Of interest, Hislop and others also noted that juvenile sand

Table 6—Mean food values of selected invertebrates and fishes[1]

Prey	Food Energy *kcal*	Protein *g*	Total Lipids [fat] *g*
Squid Mixed species (Loligoidae and Ommastrephidae)	92	15.58	1.38
Shrimp Mixed species (Penaeidae and Pandalidae)	106	20.31	1.73
Pacific Herring *(Clupea harengus pallas*i)	195	16.39	13.88
European Anchovy (*Engraulis encrasicholus*)	131	20.35	4.84
Pacific Rockfish Mixed species *(Sebastes* spp.)	94	18.75	1.57

[1] Amounts in 100-g raw samples, edible portion (Exler 1987)

eels (<10 cm) which have low body weights and high water content seemed, on purely energetic grounds, to be low-quality food. Because many different seabird species use sand lance in their diet, it may be that the overall abundance and availability of these fish compensates for the low energy value. Sand lance may also contain essential nutrients which seabirds have a need for, and the higher water content may also be important physiologically. The estimation of total energy content is complicated by dehydration of fish specimens; thus, Montevecchi and Piatt *in* Hislop and others (1991) urged seabird biologists to compare dry weight energy densities across studies. Both sets of researchers also noted the value of including wet calorific values as well.

The work of Hislop and others (1991) provides data for comparison of energy values between sand eel and herring which indicates that herring have much higher total energy value than sand eel (*table 7*). Unfortunately, there is no data available for both herring and sand eel of murrelet nestling prey size (60.1–120.0 mm) in July or August to allow a more relevant comparison.

Roby (1991) studied the diet and postnatal energetics in three species of plankton-feeding seabirds. Lipid-rich diets were associated with shorter brooding periods, higher rates of nestling fat deposition, and larger lipid reserves at fledging. The energy cost of growth was a relatively minor component of nestling energy budgets; most assimilated energy was allocated toward maintenance and fat deposition. Once growth requirements for protein had been met, any additional assimilated protein was metabolized to meet maintenance costs, and the energy saved was stored as fat. High lipid diets were associated with higher rates of lipid deposition by chicks, but not higher growth rates. Instead, constraints operating at the level of tissues are apparently responsible for most of the variation in growth rate among seabirds. Large lipid reserves at fledging presumably enhance post-fledging survival.

Discussion

Conservation and recovery of the murrelet will depend in part on a better understanding of the interaction between the factors affecting the species inland and at sea. The studies described in this chapter have shed some light on this relationship and have indicated the need for comprehensive management of marine resources and inland nesting habitat.

There is a need for additional study of murrelet diet, especially in the southern end of its range. Winter diet studies are also needed to help understand why some murrelet populations disperse to other locales during the non-breeding season. Comparison of prey abundance and composition between breeding and non-breeding foraging areas may help explain these movements.

Additionally, more research on the use of inland lakes and estuaries as foraging sites is needed, across all seasons. This aspect of the murrelet's life history has not received adequate attention except by Carter and Sealy (1986) and Hobson (1990). Though there are few large inland lakes in the coastal area of Washington, Oregon, and California,

Table 7—Calorific values (kJ/g) and total energy content (kJ) of Lesser sand eel (Ammodytes marinus) and Atlantic herring (Clupea harengus)[1]

Fish	Mean length	Collection month	Dry calorific value	Wet calorific value	Wet weight	Total energy content
	cm		*kJ/g*	*kJ/g*	*g*	*kJ*
Lesser sand eel	16.5	June	25.8	6.9	13.5	93.2
Atlantic herring	15.5	August	28.9	7.5	41.6	312

[1] Data from Hislop and others (1991)

there are numerous coastal lagoons and estuaries which may be important to murrelets.

Intensive studies on factors affecting sand lance distribution and abundance are needed, as well as further exploration of the food web of this species. The importance of this little-studied fish in the diet of murrelets from Alaska to California certainly indicates a need for further investigation of predator-prey interactions. Monitoring of sand lance populations may prove useful for comparisons with murrelet population and productivity estimates from at-sea surveys. Sand lance recruitment could potentially serve as an indicator of murrelet reproductive success. A strong correlation was reported between number of tern chicks available for banding and recruitment of sand lance (Monaghan and others 1989). The effect of pollution and physical disturbance (dredging) on sand lance populations needs management attention (Auster and Stewart 1986, Nakata and others 1991, Pinto and others 1984). Identification of sand lance spawning areas could aid conservation of the murrelet through directed management of these sites.

The threatened and endangered status of the murrelet, coupled with the low productivity estimates, indicates the need for intensive field work in order to determine food habits without sacrificing birds. Long hours of observation of murrelets at sea catching and holding fish will be necessary, and intensive, systematic searches for beached birds could yield specimens for studies of food habits. Plankton hauls along with traditional methods of assessing marine fish can be used in areas where murrelets are actively foraging to at least determine prey abundance and composition. Video footage of prey items along with collections of fish parts from nest sites can contribute to knowledge of murrelet diet. Specimens can also be obtained from gill netting operations and oil spill events. Stomach pumping or emetics could possibly be employed, especially in conjunction with radio-telemetry studies and banding or marking operations.

The identification of important foraging areas near known murrelet nesting sites will help in the conservation of this species (Ainley and others, this volume). Human activities or influences which are detrimental to the murrelets or their prey resources could then be appropriately managed in such areas.

Clark and others (1990) compared habitat structure and the number of active nests for Red-tailed Tropicbirds (*Phaethon rubricauda*) before and after an El Niño event. An increase in availability of quality habitat post-El Niño resulted in an increase in the number of active nest sites relative to pre-El Niño breeding seasons. The data of Clark and others supported the hypothesis that suitable nest sites may limit short-term reproductive opportunities of tropicbirds and, hence, influence the rate of population growth and time course of recovery from catastrophic events such as El Niño. This has important management implications for a threatened species such as the murrelet. Inland nesting habitat becomes a very important management consideration even though the murrelet relies on the marine environment for food. A study on the Red-throated Loon (*Gavia stellata*) indicated that as distance from the ocean to the nest site increased, both density and nesting success of loons decreased (Eberl and Picman 1993). The authors suggested that the higher density of breeding loons in areas near the ocean reflected a preference by these birds for nesting grounds that are closer to their foraging areas.

Since the murrelet is a forest-nesting seabird, it is imperative to consider multiple factors when devising research and management strategies. Because of its secretive nesting habits, it has been difficult to document nest success relative to prey abundance as has been done with other seabirds. Even if adult murrelets can easily choose alternate prey species for their own diet, having abundant forage fish available during the nestling period may significantly reduce the energy demand on the adults by requiring less foraging time and fewer trips inland for feeding nestlings (Carter 1984, Carter and Sealy 1990, Cody 1973, Sealy 1975c). The juxtaposition of nesting areas and foraging areas is probably most critical as one determinant of reproductive success in years of low prey abundance. Increased foraging time of adults, long flights inland, and more numerous trips inland with small prey items would potentially reduce both adult and chick survival. Competition with other seabirds for available food is also an important factor in foraging patterns and prey selection (Ainley and Boekelheide 1990: 380; Cody 1973; Mahon and others 1992).

Marine communities have been altered by the activities of humans in conjunction with natural influences (Cairns 1992a: 39). As early as 1886, declines in fish populations in heavily fished areas seemed apparent. The notes of an expedition to Puget Sound in July 1895 contained the following anecdote regarding herring: "Exceedingly abundant. J.P. Hammand (American Angler, December 18, 1886) states that from 18-25 years ago it was not an uncommon occurrence for a 'gang' of fishermen to catch from 200-300 barrels of herring in a night on Puget Sound. Now the largest night's work is 20 barrels" (Jordan and Starks 1896). The sardine fishery in California which was discussed above is another example. The relatively new fishery went from the "palmiest days" of Cannery Row in the mid-1930's to a catastrophic drop in 1947. In response to this drastic decline, there emerged what is known today as the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program to help better manage marine resources (Ricketts and Calvin 1962: 382). The observations of Radovich (1961) are helpful: "The mere fact one can demonstrate the environment has a large effect on the catch does not imply man's effect is inconsequential. To understand man's effect, one must study the effect of man. However, a satisfactory understanding may never be achieved so long as one fails to recognize the existence of some of the other factors constantly confusing his data. The effects of environment and man on fish populations are not mutually exclusive." The long history of fishing activity in the North Sea produced steep declines followed by increases when fishing pressure diminished. Such events resulted in Sir Alister Hardy's remark: "Certainly no one can deny that over-fishing exists; we must find the best way to remedy it" (Hardy 1965: 247-248).

The scale-deposition studies described above provide evidence that abundance of coastal pelagic fish species varied considerably before the inception of modern fisheries. Environmental factors and trophic-level interactions contribute to the naturally dynamic state of marine ecosystems. Fishing has, however, probably exacerbated the natural variability in recent decades because reduced stock size and loss of old fish, which is an inescapable result of fishing, increase the speed and magnitude of population decreases during periods of poor reproduction. Approaches to fishery management based on equilibrium or steady-state concepts that ignore variability in abundance have a long history of failure for coastal pelagic species in many regions of the world (Troadec and others *in* Anonymous 1993). Managers should expect considerable interannual variation in abundance and yields and should curtail fisheries to protect the long-term health of the stock when necessary. Chaotic ecosystems appear to require reliance on management that is beneficially adaptive rather than manipulative. The possibility of detailed predictions is effectively ruled out, and many factors, including socioeconomic ones, must be used when modeling populations, ecosystems, and fishery impacts (Wilson and others 1991).

Throughout its range, the murrelet consumes a very diverse group of prey resources, especially when one considers the limited studies which have been done to date. This indicates great flexibility in prey choice and a high capability for prey-switching behavior. This would make adaptive sense given the multiple factors affecting prey availability each year and the oceanographic differences found offshore from forest nesting habitat throughout the range of the species. It also indicates that El Niño events would not be expected to cause catastrophic population fluctuations or declines, especially in the long term. Given the variability in frequency and intensity of El Niño events, murrelet production could be lower than "normal" in some years as has been demonstrated for many other seabirds. But, like other seabirds, the murrelet has evolved with this phenomenon and can likely change its foraging behavior and food preferences to some degree in order to utilize available resources (Carter 1984, Croll 1990, Krasnow and Sanger 1982, Sanger 1987b, Sealy 1975c). Additionally, the long life span of the species allows for adequate reproduction and dynamic equilibrium of the population, even in the face of low reproduction in some years. However, cumulative impacts in localized areas over a short time period could cause serious population declines or possibly even extirpations.

Research should continue to identify bottlenecks to recovery; "scientifically approachable" and "practically realizable" studies should be done along with attempts at "integrated management of the marine ecosystem as a whole" (Holt 1993). A lack of information on the functioning of "natural systems" (Willers 1993) should not prevent comprehensive research or recovery actions in the future, but instead should help guide more unified study efforts. Biologists have long recognized the need to integrate seabird and marine science (Ainley and Sanger 1979, Furness 1984, Munro and Clemens 1931, Sealy 1990, and others) and the excellent treatise on the matter by Cairns (1992b) should help guide marine ecosystem research and management in the future.

Managers and researchers today are faced with the listed or sensitive management status of the murrelet and limited financial resources to conduct the necessary studies. It is now more important than ever to pool resources and seek innovative ways to conduct the necessary research. Mitigation banking policies imposed on commercial fishing and timber industries, coupled with damage assessment rewards, could help gather research funds and support the large-scale studies proposed by Nisbet (1979) and Vermeer (1992). Research monies alone are not recognized as adequate mitigation for negative impacts to natural resources, but funds derived from such policies could certainly play a stronger role in the conservation and recovery of the murrelet than has occurred up to this point.

These ideas are not new (Drury 1979, Nisbet 1979), but implementation has yet to occur on a meaningful scale. In the words of Drury (1979: 136): "Experience in Europe and in New England suggests that if reasonable limitations are set on human activities and that if adequate money charge is made against those who profit by economic development to defray full social costs, wildlife can continue to do well. In most cases where damage has occurred it is because those who administer the public institutions have failed to include consideration of the common property resources".

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