POPULATIONS, FEEDING ECOLOGY AND MOLT OF STELLER'S EIDERS

MARGARET R. PETERSEN

ABSTRACT.—This study considers the temporal and spatial distribution of Steller's Eiders (*Polysticta stelleri*) during molt along the north side of the Alaska Peninsula from Port Heiden to Bechevin Bay. Subadult eiders molted primarily at Nelson Lagoon, adult males at Nelson Lagoon and Izembek Bay, and adult females primarily at Izembek Bay. Only a few eiders used Bechevin Bay, Seal Islands, and Port Heiden. Although the flightless period overlapped among different age and sex classes, subadults were flightless first, then adult males, and last, adult females. Eiders maintained spatial and temporal separation during the flightless period, thereby reducing competition for food resources.

Eiders at Nelson Lagoon were observed feeding only by head-dipping during the pre-flightless period in 1979, a significant change from 1977 when they fed both by diving and dipping. During both 1977 and 1979 eiders foraged for approximately equal amounts of time during each stage of molt. Foods consisted primarily of bivalve mollusks and amphipods. These foods were consumed in different proportions before and after the wing-feather molt, with mussels being most important when eiders were growing remiges. Comparisons between the amount of energy in blue mussels (*Mytilus edulis*), clams (*Macoma balthica*), and gammarid amphipods showed that mussels yield the most energy per gram of whole wet weight. Apparently Steller's Eiders have adjusted to the increased energy demands of molt by eating invertebrates with high caloric content, rather than by increasing the amount of time feeding.

Steller's Eiders (Polysticta stelleri) nest across northern Siberia, northern Alaska, and the Yukon-Kuskokwim Delta in western Alaska (Bellrose 1976). Although formerly abundant on the Yukon Delta (Conover 1926, Brandt 1943, Olson 1950), these ducks are no longer common breeding birds in either western or northern Alaska, and their current primary breeding area is in northern Siberia. Birds undergo molt of the remiges in large concentrations in northwest Asia (Kistchinski 1973) and along the Alaska Peninsula. Returns of birds banded at Izembek Bay suggest that the majority of birds molting at Izembek Bay nest in northern Siberia (Jones 1965).

These eiders are among the most conspicuous birds found in the bays and lagoons along the north side of the Alaska Peninsula. However, information on the importance of those lagoon systems and the nature of their use by eiders is limited to observations at Izembek Bay by Jones (1965) and at Nelson Lagoon by Petersen (1980). Nothing has been reported on the size and distribution of populations, habitat characteristics, food preferences, behavior, and physiology of Steller's Eiders when along the Alaska Peninsula during the post-

breeding season. This basic information is considered essential for evaluating the potential effects of development of petroleum resources in the Bering Sea, because of the apparent critical importance of the lagoon systems to eiders and the vulnerability of eiders and their foods to pollution by oil.

This study was designed to evaluate the use and importance of lagoon systems to Steller's Eiders while they are molting along the Alaska Peninsula. My specific objectives were to: determine the number, age, and sex of birds molting in lagoon systems from Port Heiden to Bechevin Bay; determine the timing of the remigial molt; and, evaluate the food habits and feeding behavior of eiders at Nelson Lagoon in relation to the lipid and protein content of the primary foods.

STUDY AREA

The study area consisted of five major lagoons and bays along the north side of the Alaska Peninsula from Port Heiden to Bechevin Bay (Fig. 1). Izembek Bay (344 km²) is the largest of these lagoon systems, and is followed in size by Bechevin Bay (241 km²), Port Heiden (204 km²), Nelson Lagoon (141 km²), and Seal Islands (50 km²) (Fig. 1). Each lagoon and bay system is characterized by extensive shallow areas of mud, sand, and sand-gravel flats frequently exposed at low tide, and

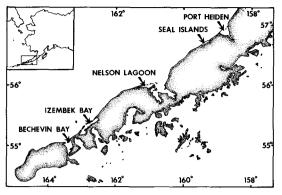


FIGURE 1. Study area along the north side of the Alaska Peninsula.

barrier islands or spits that partially protect the lagoons and bays from the open sea. Eel grass (*Zostera marina*) grows in extensive beds in Izembek Bay and Bechevin Bay, and locally within other lagoons. Mean diurnal tide on the study area ranges from 3.8 m at Port Heiden to 1.1 m at Bechevin Bay.

Nelson Lagoon, the primary study area, has been described by Gill and Jorgensen (1979) and Petersen (1980). The lagoon is shallow, with extensive flats (47%) of the lagoon) exposed at mean low tide. Intertidal substrates range from mud to a mixture of sand and gravel. The daily tidal regime is two lows and two highs with a mean diurnal range of 3.2 m. Blue mussel (Mytilus edulis), a clam—balthica macoma (Macoma balthica), and polychaete worms (primarily Eteone longa) dominate the epibenthic fauna. During most winters, shore-fast ice forms in the lagoon and the scouring action of ice during break-up in the spring may remove most one-year old and older blue mussels. However, in the springs of 1978 and 1979 there was no ice movement out of the lagoon and several age classes of mussels survived.

METHODS

DISTRIBUTION, AGE, AND SEX IDENTIFICATION

In 1977 observations were limited to Nelson Lagoon where censuses were conducted every third week from 15 April to 15 October. In 1979 I conducted censuses between 17 August and 2 October, and extended the survey to all lagoon systems. Birds were counted from an airplane flown at 50-75 m over lagoon systems between 1.5 hours before and after low tide. Molt status, age, and sex ratios were determined during the aerial surveys. I verified aerial surveys by surface observations and from specimens collected at Nelson Lagoon and Izembek Bay. I considered subadult age classes as one group, because yearlings and second-year birds were difficult to distinguish except when in alternate plumage or in the hand (Palmer 1976). Adult and thirdyear males were distinguishable from yearlings and second-year males in all plumages. I could not distinguish third-year males in basic plumage from older males, and included them in the adult category. I identified adult females by collecting birds and examining live birds during a banding drive. Hatching-year birds were identified by their basic I plumage.

FEEDING BEHAVIOR

I observed feeding and roosting birds at Nelson Lagoon with a spotting scope every three days from 17 April to 15 October 1977, and from 28 June to 30 September 1979. The activity of each bird in view was recorded every two hours from 08:00 to sunset in 1977 (N = 42 days), and from 06:00 to sunset in 1979 (N = 23 days). Descriptive terminology of feeding methods is that used by Bryant and Leng (1975).

FOOD HABITS

I collected 96 eiders to determine the type of food eaten in Nelson Lagoon. Samples of three birds were taken from feeding flocks every three weeks between 17 April and 15 October 1977. Nine birds were taken September-October 1976 and four birds in September-October 1978. Samples of five birds of each age-sex category were taken every two weeks between 25 June and 1 October 1979. Immediately after collection, I injected the esophagus, proventriculus, and ventriculus of each bird with 10% buffered formalin to halt digestion and preserve food items. After preservation these organs were removed and stored in 50% 2-propanol. Food items were sorted and identified to species when possible. I have presented data as the mean of volumetric percentages (aggregate percentages; see Swanson et al. 1974) for each sampling period.

INVERTEBRATE SAMPLES

Samples of *Macoma balthica* and *Mytilus edulis* were collected at Nelson Lagoon in 1979 at two-week intervals for later determination of their protein, fat, carbohydrate, and ash content. I randomly sampled mussels at low tide by removing entire clumps of them until a 12-l container was filled. From this collection a 100-g sample of whole *M. edulis* 1–30 mm in length was removed and rinsed, then immediately frozen in fresh water. I also collected *Macoma* at low tide. Areas were randomly selected on a mud-sand flat, and the substrate passed through a 0.5 mm sieve until a sample of at least 100 g was obtained. Collections were made during minus tides in order to obtain sufficient samples of clams.

ANALYSIS OF PROTEIN, FAT, CARBOHYDRATE, AND ASH IN FOOD SAMPLES

Three replicates of each sample of Mytilus edulis and Macoma balthica were analyzed for crude protein, crude fat, nonstructural carbohydrate (TNC), and ash content. Samples were prepared for analysis by removing the shell, then drying the contents at 65°C. Crude protein was determined by block digestion with a H₂SO₄H₂O₂ digestion medium containing selenous acid. The converted ammonium ion was reacted with alkaline phenol blue complex, and crude protein content was determined colorimetrically with a Technicon Auto-Analyzer II System (Anonymous 1976). Crude fat was determined gravimetrically by ether extraction (Horwitz 1970), Nonstructural carbohydrates were determined by a modified Weinmann method with reducing power measured colorimetrically on the Auto-Analyzer II. Ash was determined gravimetrically as the difference in weight before and after igniting at 500°C in a muffle furnace.

STATISTICAL ANALYSES

Data on foods eaten, components of invertebrate samples, and observations of feeding behavior are presented as percentages. All percentage data were transformed to angular transformation values in order to meet the assumptions of the analysis of variance (Sokal and Rohlf 1969) and analysis of variance tests performed on transformed data. Data presented in tables and figures are untransformed.

TABLE 1.	Maximum number of Steller's Eiders observed in lagoons and bays from Port Heiden to Bechevin
Bay.	

	1977	1979						
	Nelson Lagoon	Bechevin Bay	Izembek Bay	Nelson Lagoon	Seal Islands	Port Heiden	Total	
Hatching year	0	16	4,970	18,265	0	9,000	31,951	
Pre-flightless subadults ¹	26,364	_	·	·		_	·	
Flightless subadults	52,576	0	4,198	12,985	1,180	655	19,018	
Post-flightless subadults	6,104	0	7	3,183	375	0	3,565	
Pre-flightless adult males	1,244	0	9,986	12,985	3,948	65	29,984	
Flightless adult males	30,630	0	32,567	3,045	515	120	36.247	
Post-flightless adult males	54,943	1	2,293	10,041	144	0	12,479	
Pre-flightless adult females	0	0	43	0	0	0	43	
Flightless adult females	0	0	4,321	476	0	0	4,797	
Post-flightless adult females ²	0	0	0	94	0	0	94	

¹ No aerial surveys were conducted before the flightless period of subadults in 1979.
² Most adult females had not completed remigial growth before the last aerial survey in 1979.

RESULTS

SIZE AND DISTRIBUTION OF POPULATION

As suggested previously (Petersen 1980), the age and sex classes of Steller's Eiders are separated spatially during the molt. Izembek Bay is clearly the most important area for molting adult females (Table 1). In neither year were significant numbers of flightless females seen at Nelson Lagoon, nor were they found in lagoons other than Izembek Bay in 1979 (Table 1).

The data suggest that both Izembek Bay and Nelson Lagoon can be important molting areas for adult male eiders (Table 1). Before males lost their remiges in 1979, 48.1% were observed in Nelson Lagoon. However, 89.8% of the flightless birds were recorded at Izembek Bay in 1979. After completing molt of the remiges, males staged briefly at Nelson Lagoon, then left the lagoon system.

Subadults molted at Nelson Lagoon in preference to all other lagoons. Over 52,000 subadults molted at Nelson Lagoon in 1977, and 68.3% of 19,018 molted there in 1979 (Table 1). Subadults, like adult males, disappeared from there after completing growth of the remiges. They were not found in any of the lagoon systems after regaining flight.

The number of birds in lagoon systems along the north side of the Alaska Peninsula differed between years. In 1977 the maximum counts of adult males and subadults at Nelson Lagoon totaled over 100,000, whereas in 1979 only 92,000 birds of both sexes and all ages were counted along the entire north side of the Alaska Peninsula (Table 1). The number of subadults was reduced by 58.2% from 1977, and the number of adult male eiders was down by at least 35.6%. However, more females were seen in 1979, possibly because surveys were extended to other lagoons. Hatching-year birds were not observed in 1977, but 31,951 were counted in 1979.

MOLT CHRONOLOGY

In 1977 subadults arrived in the lagoon areas at least three months before losing remiges, and in 1979 were present on 25 June, at least 1.5 months before losing remiges (Table 2 and Fig. 2). In contrast, adult males lost remiges soon after their arrival in 1977 and in 1979, although their time of arrival varied by almost a month (Table 2).

Molt in 1977 began almost a month earlier in subadults than in adult males, but in 1979 began almost simultaneously because the flightless period of subadults was later and that of adult males was earlier than in 1977 (Fig. 2). In 1979 the flightless period of adult males was twice as long as in 1977, suggesting that all adult males did not arrive simultaneously, as they did in 1977. The flightless period for adult females coincided with the latter half of the molt period of adult males, and extended about three weeks beyond the time the last male completed remigial growth.

FEEDING BEHAVIOR

The amount of time birds spent foraging during each stage of the tide did not differ

 TABLE 2.
 Arrival dates of Steller's Eiders at Nelson Lagoon.

	1977	1	1979		
	First	Peak	First	Peak	
Hatching year			17 Sept.	27 Sep	
Subadults	27 April	22 July	_ `	4 Aug	
Adult males	4 Aug.	16 Sept.	7 Aug.	11 Aug	
Adult females		_	6 Sept.	27 Sep	

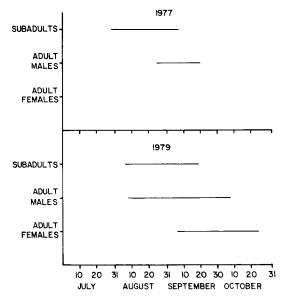


FIGURE 2. Dates when Steller's Eiders were flightless. Dates are calculated from observations of birds and verified from measurements of growing primaries (Petersen, unpubl. data).

significantly between years, or between stages of wing-feather molt. Most foraging occurred within plus or minus 2 h of low tide (Fig. 3).

Eiders fed both by dipping their heads in shallow water and by diving for food, spending more time head-dipping at low tide (Fig. 4). In 1977 the mean percentage of time birds fed by dipping did not vary significantly between stages of wing-feather molt. However, in 1979 birds fed almost exclusively by dipping until they began remigial molt (Fig. 4a), possibly reflecting an increased availability of sessile mussels as a result of a mild winter. The amount of time flightless birds foraged by head-dipping did not differ significantly between 1977 and 1979 during any stage of the tide (Fig. 4b). Although birds fed by diving after completing remex growth, birds in 1979 fed significantly more by head-dipping during the primary feeding times (Fig. 4c).

FOOD HABITS

Steller's Eiders ate substantially the same foods in 1977 and 1979, with blue mussels, other bivalves, and amphipods providing the main sources of nutrition. The relative proportion and amount of bivalve mollusks in the diet increased sharply at the start of the pre-basic molt and growth of remiges, and remained high until flight was regained and remiges fully developed (Table 3). During this period the amount of bivalve mol-

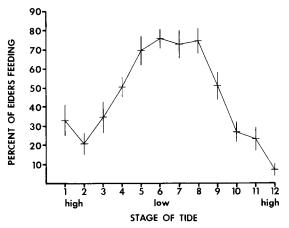


FIGURE 3. Percent (mean \pm SE) of Steller's Eiders feeding during each stage of the tide in 1977 and 1979.

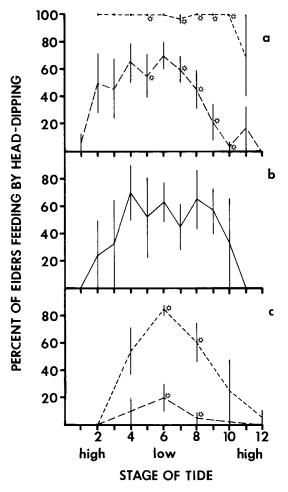


FIGURE 4. Percent (mean \pm SE) of eiders feeding by head-dipping in relation to the stage of the tide: a. before the flightless period, b. when flightless, c. after the flightless period. Solid line, 1977 and 1979; combined, large dashed line, 1977; small dashed line, 1979. * Significant difference (P < 0.05) between years at that tide stage.

	Num- ber of	Aggregate percentage		
	eiders	Mean	SE	Range
Pre-molt				
13 May 1977	7	7.8	3.8	0-30.0
10–25 June*				
1977	4	39.6	10.7	18.2 - 62.5
1979	4	94.5	2.2	89.5 - 100
5–11 July				
1977	3	68.2	10.6	44.7 - 86.1
1979	6	81.3	13.1	19.0 - 100
23 July–6 August				
1977	3	72.7	7.8	59.0-86.2
1979	12	80.2	8.1	0.5 - 99.0
Growing remiges				
1977	5	91.4	5.6	70.0-100
1978	2	98.0	2.0	96.1-100
1979	25	80.4	6.1	0.5 - 100
Remex growth com	pleted*			
1976	9	10.8	9.1	0-65.9
1977	6	52.9	12.8	11.3 - 97.4
1978	4	93.8	4.6	80.0-99.0
1979	5	0.4	0.1	0.5 - 0

TABLE 3. Amounts of bivalve mollusks eaten by Steller's Eiders at Nelson Lagoon from May-October.

TABLE 4. Amounts of amphipods eaten by Steller's Eiders at Nelson Lagoon from May–October.

	Num- ber of	Aggregate percentage			
	eiders	Mean	SE	Range	
Pre-molt				_	
13 May 1977	7	85.7	6.0	50.0 - 95.5	
10–25 June*					
1977	4	54.6	12.7	25.0 - 77.9	
1979	4	0.2	0.1	0 - 0.5	
5–11 July*					
1977	3	29.4	12.5	11.1-53.2	
1979	7	3.8	3.5	0-25.0	
23 July-6 August	*				
1977	3	25.9	7.6	12.1 - 38.5	
1979	12	4.0	2.2	0-25.0	
Growing remiges					
1977	5	0.0	0.0	0	
1978	2	0.0	0.0	0	
1979	25	2.6	1.5	0-37.0	
Remex growth com	pleted				
1976	9	75.4	14.4	0-100	
1977	6	32.9	13.7	0-88.7	
1978	4	0.3	0.2	0-0.8	
1979	5	47.5	20.8	0.5 - 99.0	

* Significant difference (P < 0.05) between years.

* Significant difference (P < 0.05) between years.

lusks eaten did not differ significantly between 1977 and 1979. However, the amounts of bivalves eaten by birds that had completed remigial growth differed significantly between years (F = 17.11, df = 3, 19, P < 0.05; Table 3). In 1979, hatchingyear birds with full flight capability ate significantly fewer bivalve mollusks than flightless birds collected during the same period (F = 38.02, df = 1, 28, P < 0.05).

The amounts of amphipods eaten by eiders in the period preceding molt of the remiges differed significantly between years (Table 4). In both years, eiders ate small amounts of amphipods when flightless and more of them, but not significantly, after completing molt.

PROTEIN, FAT, CARBOHYDRATE, AND ASH ANALYSIS

The percent of crude protein, crude fat, and nonstructural carbohydrates (TNC) found in *Mytilus edulis* in 1979 varied significantly between samples (protein, F = 7.88, df = 6, 14, P < 0.001; fat, F = 11.04, df = 6, 13, P < 0.001; TNC, F = 6.81, df = 7, P < 0.025). The highest levels of protein occurred in July and September, and the highest levels of fat occurred in July (Fig. 4). Carbohydrates remained relatively constant except for low levels found in early August (Fig. 5). I found no significant differences

in the water content, ash content, or tissueto-shell ratios of *M. edulis* among samples throughout the collection period. There were also no significant differences between the kcal/g of whole mussels among samples. Mussels less than 30 mm in length averaged 1.52 ± 0.05 kcal/g whole wet weight.

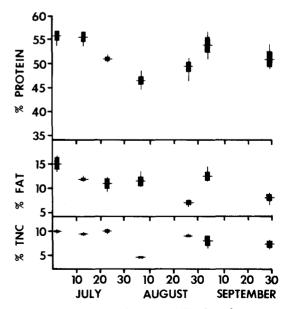


FIGURE 5. Percent (mean \pm SE) of crude protein, crude fat, and nontransferable carbohydrate (TNC) in *Mytilus edulis* in 1979.

The amounts of crude protein, crude fat, TNC, and ash in *Macoma balthica* did not vary significantly among collections. As with *Mytilus edulis*, there were no significant differences in water content, ash content, or shell-to-tissue ratio among collections of these clams. Similarly, the kcal/g of whole clams did not vary significantly among samples, and averaged 0.054 ± 0.004 kcal/g whole wet weight.

DISCUSSION AND CONCLUSIONS

DISTRIBUTION OF MOLTING STELLER'S EIDERS

In Alaska the lagoons along the north side of the Alaska Peninsula appear to be the most important molting areas for Steller's Eiders in most years (Jones 1965; this study). Observations of flightless eiders at Cape Peirce (Petersen, unpubl. data) and Saint Lawrence Island (Fay 1961) suggest, however, that several hundred birds may molt elsewhere along the coast of Alaska. The difference in numbers between 1977 and 1979 indicates that in some years several thousand eiders may molt in northeast Asia (Kistchinski 1973), but those areas for molting have not been adequately surveyed. Along the Alaska Peninsula, Izembek Bay and Nelson Lagoon are clearly most important for eiders during remigial molt.

The variation in timing of arrival and molt of adult eiders on the Alaska Peninsula may partly be related to conditions on the breeding areas and the timing of nesting (Jones 1965). In order to understand more fully the eiders' timing of arrival at the Alaska Peninsula, more studies are needed on the breeding biology and nesting chronology of the population in northern Siberia.

The spatial separation of molting birds may be partially explained by the quantity of food eaten by the eiders. During the molting period, subadults may remove between 1.2 and 6.2 metric tons of Mytilus edulis per day from Nelson Lagoon and adult males may remove an additional 3.6 metric tons. During peak population periods, more than 7.3 metric tons of mussels per day (based on 119-127 g/eider/day; see below) are being eaten by Steller's Eiders in Nelson Lagoon. Obviously, the yearly crop of *M. edulis* is important to eiders attempting to grow remiges at Nelson Lagoon. However, the standing crop (g produced per ha) of mussels at Nelson Lagoon, and the foods of eiders at Izembek Bay and the standing crop of those invertebrates must be determined before further conclusions can be made about the distribution of eiders molting in the two lagoons in relation to available foods. Furthermore, the invertebrates and the eiders at Port Heiden, Seal Islands, and Bechevin Bay must be studied in detail before any conclusions can be made regarding the distribution and abundance of Steller's Eiders along the Alaska Peninsula. This research is needed before we can evaluate the potential effects of the impending development of petroleum resources in the Bering Sea.

FOODS AND MOLT ENERGETICS

The energetic cost of molt to birds that lose their remiges simultaneously is thought to be higher than in species that undergo a typical sequential molt (Hanson 1962, King 1974). Recent studies of Cackling Canada Geese (Branta canadensis minima; Raveling 1979) and Lesser Snow Geese (Anser caerulescens caerulescens; Ankney 1979) have suggested that during remigial molt geese can meet their energy needs without a loss of total body weight. Those studies suggest that geese, and possibly other waterfowl species, can meet their increased daily energy requirements by eating either more food per day or foods of higher caloric content. Steller's Eiders did not lose weight during the molt (Petersen, unpubl. data); thus, they must compensate for the higher energy needs either by increasing the amount of time feeding or by eating more nutritious foods.

Steller's Eiders require 104 kcal/day (males) to 116 kcal/day (females) to meet daily requirements of feather growth, assuming that their energetic cost during the molt is similar to that found by Prince (1979) for dabbling ducks (kcal/day for males = 121.1 $W^{0.734}$; kcal/day for females = 134.5 W^{0.734}). An eider must eat 68–76 g of Mytilus edulis (1.52 kcal/g whole wet weight; this study) each day in order to meet those energy needs. However, an eider will need to increase its energy input by at least $3.2 \times$ BMR (Prange and Schmidt-Nielson 1970) or by about 51 g of mussels for six hours of feeding to meet the extra energy needs due to the swimming associated with feeding. Thus, during the molt, an eider must eat at least 119–127 g of blue mussels to supply its minimum daily energy needs.

If an eider ate at least 60 g of *M. edulis* (the amount in the fullest bird collected), then it could meet its daily energetic needs for feather growth by eating to its capacity once during each of the two daily low tides. If an eider were to satisfy its daily energy needs by eating gammarid amphipods (0.47)

kcal/g whole wet weight; Tyler 1973), it would have to eat 413 g of amphipods each day. Thus, the eider would have to eat to capacity (85 g of amphipods) 4.9 times during the day. After the remiges are grown (for winter dabblers see Prince 1979) an eider would need to eat amphipods to its capacity 4.4 times each day. However, after the molt is complete eiders actually eat both amphipods and mussels thereby needing to completely fill their gut 1.9 to 4.4 times each day, depending on the ratio of mussels to amphipods.

An eider could increase its total caloric intake per day either by feeding longer or by eating foods that contain more energy. Eiders always feed during low tide regardless of the stage of molt, and do not significantly increase the amount of time they feed when growing remiges. The greater amount of energy needed for diving at high tide might offset any gains of increased food consumption of eiders at Nelson Lagoon. Apparently, Steller's Eiders meet the increased energetic demands of growing remiges by eating invertebrates that have a high caloric content.

ACKNOWLEDGMENTS

K. L. Muller and C. I. Adamson enthusiastically assisted in field work at Nelson Lagoon in 1979. R. E. Gill, Jr. provided his unpublished data on eiders collected in 1976 and 1978. The staff of the Izembek National Wildlife Range allowed me to participate in their annual eider banding drive, and observe Steller's Eiders in Izembek Bay. I thank B. Connet of the Migratory Bird Program, Juneau, Alaska for letting me participate as an observer during the October survey of the north side of the Alaska Peninsula. George Mitchell of the Palmer Plant and Soils Laboratory, Agricultural Experimental Station, University of Alaska analyzed the invertebrate samples. D. V. Derksen, C. J. Lensink, J. Lewis, J. Morrison, G. A. Sanger, and D. Schamel reviewed various versions of this manuscript and provided helpful comments.

In 1977, this study was supported by the Bureau of Land Management under contract to the National Oceanic and Atmospheric Administration as part of the Outer Continental Shelf Environmental Assessment Program. In 1979, field work was supported by the U.S. Fish and Wildlife Service, Division of Wildlife Ecology and Research, Washington, D.C.

LITERATURE CITED

ANONYMOUS. 1976. The simultaneous determination of nitrogen and phosphorous on BD acid digests. Technicon Instruments Corp., Tarryton, NY.

ANKNEY, C. D. 1979. Does the wing molt cause nu-

tritional stress in Lesser Snow Geese? Auk 96:68-72.

- BELLROSE, F. C. 1976. Ducks, geese and swans of North America. Stackpole Books, Harrisburg.
- BRANDT, H. 1943. Alaska bird trails: an expedition by dog sled to delta of the Yukon River at Hooper Bay. Bird Research Foundation, Cleveland.
- BRYANT, D. M., AND L. LENG. 1975. Feeding distribution and behaviour of Shelduck in relation to food supply. Wildfowl 26:20–30.
- CONOVER, H. B. 1926. Game birds of the Hooper Bay region, Alaska. Auk 43:162–180.
- FAY, F. H. 1961. The distribution of waterfowl to St. Lawrence Island, Alaska. Wildfowl 12:70-80.
- GILL, R. E., JR., AND P. D. JORGENSON. 1979. A preliminary assessment of timing and migration of shorebirds along the northcentral Alaska Peninsula. Stud. Avian Biol. 2:110–120.
- HANSON, H. C. 1962. The dynamics of condition factors in Canada Geese and their relation to seasonal stresses. Arct. Inst. of N. Am. Tech. Pap. No. 12.
- HORWITZ, W. [ED.]. 1970. Official methods of analysis of the Association of Official Analytical Chemists. Association of Official Analytical Chemists, Washington, DC.
- JONES, R. D., JR. 1965. Returns of Steller's Eiders banded in Izembek Bay, Alaska. Wildfowl 16:83-85.
- KING, J. F. 1974. Seasonal allocation of time and energy resources in birds, p. 4–70. In R. A. Paynter, Jr. [ed.], Avian energetics. Nuttall Ornithol. Club Publ. 15.
- KISTCHINSKI, A. A. 1973. Waterfowl in northeast Asia. Wildfowl 24:88–102.
- OLSON, S. T. 1950. A study of goose and brant nesting on the Yukon-Kuskokwim Delta. Unpubl. admin. report, U.S. Fish Wild. Serv., Juneau, AK.
- PALMER, R. S. [ED.]. 1976. Handbook of North American birds. Vol. 3. Yale Univ. Press, New Haven.
- PETERSEN, M. R. 1980. Observations of wing-feather moult and summer feeding ecology of Steller's Eiders at Nelson Lagoon, Alaska. Wildfowl 31:99– 106.
- PRANGE, H. D., AND K. SCHMIDT-NIELSEN. 1970. The metabolic cost of swimming in ducks. J. Exp. Biol. 53:763–777.
- PRINCE, H. H. 1979. Bioenergetics of postbreeding dabbling ducks. In T. A. Bookhout [ed.], Waterfowl and wetlands—an integrated review. Proc. Wildlife Society 1977 Symp., Madison, WI.
- RAVELING, D. G. 1979. The annual cycle of body composition of Canada Geese with special reference to control of reproduction. Auk 96:234–252.
- SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. W. H. Freeman, San Francisco.
- SWANSON, G. A., G. L. KRAPU, J. C. BARTONEK, J. R. SERIE, AND D. H. JOHNSON. 1974. Advantages in mathematically weighting waterfowl food habits data. J. Wildl. Manage. 38:302–307.
- TYLER, A. V. 1973. Caloric values of some North Atlantic invertebrates. Mar. Biol. 19:258–261.

U.S. Fish and Wildlife Service, Marine Bird Section, Seattle National Fisheries Research Center, 1011 E. Tudor Road, Anchorage, Alaska 99503. Accepted for publication 23 February 1981.