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## Diet and body condition of spectacled eiders wintering in pack ice of the Bering Sea

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**Abstract** Spectacled eiders (*Somateria fischeri*) winter among leads in the Bering Sea pack ice, where they dive 40–70 m for benthic prey. During the first icebreaker cruises into that area, esophagi of collected eiders contained only clams, mostly *Nuculana radiata*, with no trace of the once-dominant *Macoma calcareea*. Alternative prey used elsewhere (snails, amphipods, other bivalves) were available but not eaten. Eiders ate mainly *N. radiata* 18–24 mm long, although *M. calcareea* of this length contained 62% more energy. Percent body lipid of eiders averaged  $12 \pm 3\%$  (SD) for 26 adult males and  $14 \pm 3\%$  for 12 adult females. Mean body mass ( $\pm$ SE) of these males in late March ( $1,688 \pm 21$  g) was higher than reported for 53 males after arriving at breeding areas in late May ( $1,494 \pm 14$  g). Body mass of these females ( $1,550 \pm 35$  g) was lower (but not significantly) than reported for 11 females upon arrival at breeding sites ( $1,623 \pm 46$  g). In 1999, the last spectacled eiders left the wintering area on 21 April, 4–8 weeks before their typical arrival at breeding sites. Their location is unknown in the interim, when habitats used appear critical to acquiring reserves for reproduction.

### Introduction

Spectacled eiders (*Somateria fischeri*) nest on the northeast coast of Siberia, the North Slope of Alaska, and the Yukon-Kuskokwim (Y-K) Delta (Fig. 1). In the late 1990s, the total population was about 360–375,000 (Larned and Tiplady 1999). Trends in the Russian

subpopulation (about 90% of all current breeders) are unknown (Petersen et al. 2000). Numbers on the North Slope (5% of all breeders) from 1993 to 1998 were roughly stable (Larned and Tiplady 1999), but were thought to have declined (Petersen et al. 2000). From the early 1970s to the early 1990s, numbers of pairs on the Y-K Delta (currently 5% of all breeders) declined by 96% from 48,000 to 2,000, apparently stabilizing at that low level (Stehn et al. 1993; Ely et al. 1994; Petersen et al. 2000). As a result, in 1993 this species was listed as Threatened under the US Endangered Species Act.

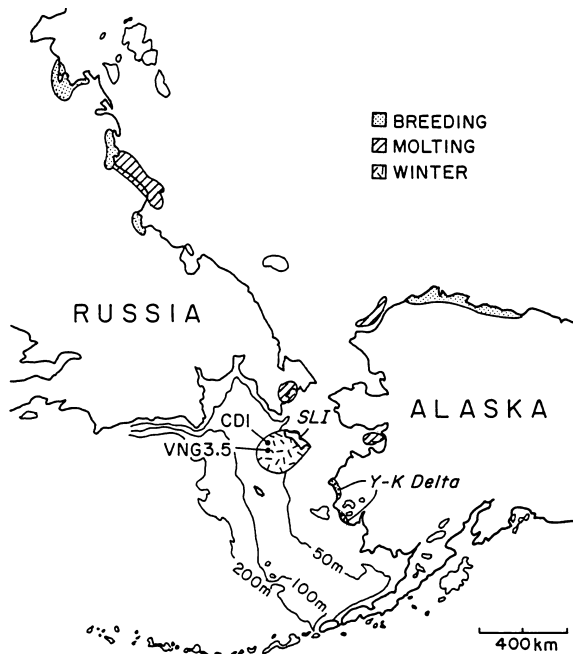
Reasons for decline on the Y-K Delta are unclear. Lead poisoning causes appreciable mortality of hens and ducklings during the breeding season, but up to 46% of the annual mortality of adult females appears to occur in the nonbreeding period (Flint and Grand 1997; Grand et al. 1998; Flint et al. 2000). Previous lead exposure might hinder reserve storage during the postbreeding period (e.g., Hohman et al. 1990), but overt signs of toxicity from lead acquired on nesting areas should become negligible within 5–7 weeks (Finley et al. 1976; Mautino and Bell 1986, 1987; but see Dieter and Finley 1978). Regardless of the mechanism, modeling indicates that a major limitation on the Y-K Delta population is adult mortality (US Fish and Wildlife Service 1996), much of which occurs away from breeding areas (Flint et al. 2000).

From late December to mid-April, the only known wintering area of spectacled eiders is among leads in the pack ice south of St. Lawrence Island in the Bering Sea (Fig. 1). There they dive 40–70 m in near-freezing water for benthic prey. Air temperature is often below  $-10^{\circ}\text{C}$ , with windspeeds commonly  $> 55 \text{ km h}^{-1}$  and at times well over  $100 \text{ km h}^{-1}$ . These challenging foraging conditions are offset by very high densities of benthic organisms (Grebmeier and Cooper 1995). At least 65% of benthic biomass there ( $\text{g C m}^{-2}$ ) is clams, mainly *Nuculana radiata*, *Macoma calcareea*, and *Nucula belloti* (Grebmeier et al. 1989; National Research Council 1996).

*M. calcareea*, which dominated clam biomass in the 1950s and early 1960s, had been replaced in dominance

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**Fig. 1** Breeding, molting, and wintering areas of spectacled eiders (after Petersen et al. 2000). Eiders were collected mostly at station CD1 southwest of St. Lawrence Island (SLI). Benthic samples were taken with a dredge and a van Veen grab at stations CD1 and VNG3.5. From December to April, pack ice covers a variable area, with the southern edge of the pack ranging from near St. Lawrence Island to the edge of the Continental Shelf at the 200-m isobath

by *Nuculana radiata* by the late 1980s (Sirenko and Koltun 1992; National Research Council 1996). Studies begun in the mid-1980s have shown declines in the biomass per square meter and mean sizes of clams (Grebmeier and Dunton 2000). These changes reflect widespread alterations in the Bering Sea food web which appear related to climate change, especially an oceanic regime shift to warmer conditions in 1976–1977 (National Research Council 1996) and another regime shift in 1989 (Hare and Mantua 2000).

Although population trends in Siberia, and on the North Slope before 1993, are unknown, the decline of spectacled eiders on the Y-K Delta appears roughly concurrent with long-term trends in the Bering Sea benthos. This observation raises questions about effects of benthic changes on the winter diet of eiders and their late-winter body condition. In common eiders (*S. mollissima*), adequate fat stores of females are important to nest success, brood attendance by hens, and duckling survival (Korschgen 1977; Bustnes and Erikstad 1991; Erikstad et al. 1993; Bustnes et al. 2002; Oosterhuis and van Dijk 2002), and many females do not nest in years when feeding conditions on wintering areas are depressed (Coulson 1984). Body condition of breeding females may not fully reveal such effects, as females in poor condition might not appear on nesting areas. In common eiders, feeding conditions before arrival at nesting sites appear critical to acquiring reserves for breeding (Pehrsson 1975; Milne 1976; Parker and Holm

1990; Christensen 2000; Guillemette 2001; Oosterhuis and van Dijk 2002). Thus, the prey relations and body condition of eiders in late winter not only reflect winter conditions that affect survival, but also appear important during the period of prebreeding conditioning. However, for spectacled eiders, there were no existing data on these issues.

In March/April 1999 and 2001, we made the first icebreaker cruises to study spectacled eiders and processes affecting their habitats in the pack ice where they winter. Here we describe their diets relative to prey availability, and their body mass and condition in late winter relative to that reported after arrival at breeding areas on the Y-K Delta.

## Materials and methods

### Body composition and diet

Spectacled eiders, which occur in large concentrations in scattered leads in the pack ice, were located with helicopters deployed from the ship. Their wintering area was first discovered only in 1995; but in each of the 5 years since when complete surveys were done, in March/April the eiders were mostly in the same area of about 40×85 km centered around the collection site in 2001 (Fig. 1; Larned and Tiplady 1999; J.R. Lovvorn, unpublished data). To avoid having to retrieve birds from open water or near thin ice at the edges of leads, we collected eiders with shotguns using 48 standard decoys and 2 automated decoys set out on the ice about 50 m from the ice edge. On 19 March 2001, we collected 39 eiders in this manner at one site (62°40.9'N, 173°22.7'W, depth 55 m), which became station CD1 (Fig. 1). All eiders that had food in their esophagi or gizzards were collected at this site. Near this site, on 22 March 2001, we salvaged one adult male and two adult females when they collided with the ship during predawn hours. One adult male was shot near a lead without decoys on 19 April 1999. All birds were frozen under ambient temperatures in the field or when placed in a freezer upon our return to the ship within 2 h of collection.

We dried the plumage of frozen eiders with a hair drier before measuring fresh body mass. We measured total length (from tip of bill to tip of tail with the bird flat on its back, minus tail length), tarsus length (from outside the tarsal-metatarsal joint to outside the tarsal-phalangeal joint when flexed at right angles), wingspan (between the tips of primaries for outstretched wings), and keel length (exposed during dissection). We sheared the feathers, and then removed the liver, kidneys, and 3–4 g of pectoral muscle for contaminant analyses; we removed the contents of the esophagus (proventriculus) and gizzard separately. Fresh masses (mean ± SD) of removed tissues were 63.6 ± 11.7 g for liver, 4.2 ± 0.5 g for both kidneys combined, and 3.7 ± 0.4 g for the pectoral muscle sample. For each individual eider, we calculated the water, protein, and lipid in removed tissues by assuming 70.4% water, 26.2% protein, and 3.3% lipid in those tissues (Raveling 1979), and added those amounts to values for the remaining carcass. The carcasses were then cut into smaller pieces and ground in an electric meat grinder. Duplicate 50- to 70-g samples of the homogenate were oven-dried at 60°C, combined and ground in a blender, and subsampled in duplicate (~5 g each) for Soxhlet extraction with ethyl ether. Two 3- to 6-g samples of the dried homogenate were ashed for 12 h at 500°C. Protein content was calculated as the difference between lipid-free dry mass and ash.

For comparison of sexes and ages, we corrected body protein for structural body size (Ankney and Afton 1988). For four structural parameters (total length, keel length, tarsus length, wingspan), we performed principal component (PC) analysis of the correlation matrix for all sexes combined. Each variable had a

positive loading (0.39–0.54) on the first principal component (PC<sub>1</sub>): eigenvalues for PC<sub>1</sub> explained 56% of total variance. We used PC<sub>1</sub> scores for each bird as a measure of body size. Regression of body protein (*PR*) on PC<sub>1</sub> scores yielded the equation  $PR = 0.3698 + 0.0165PC_1$  ( $r^2 = 0.53$ ,  $P < 0.001$ ). Protein adjusted for structural size,  $PR_a$ , was then calculated as  $PR_a = PR - (0.3698 + 0.0165PC_1) + 0.3692$ , where 0.3692 is the overall mean (kg) of *PR* ( $n = 43$ ). Body fat was not correlated with PC<sub>1</sub> scores ( $r^2 = 0.06$ ,  $P = 0.113$ ), so fat was not corrected for structural size.

We measured the length, fresh mass, and dry mass of each entire clam in esophagi (proventriculi) and gizzards (no food items except clams were found). Fragments in esophagi and gizzards (all shell material) were examined under magnification for species identification.

### Benthic samples

On 31 March 2001, we collected benthic samples under the pack ice at stations CD1 (62°40.9'N, 173°22.7'W; depth 55 m) and VNG3.5 (62°33.8'N, 173°33.4'W; depth 65 m) (Fig. 1). CD1 was the station where most eiders were collected in 2001, and VNG3.5 was the station where peak numbers of eiders were observed in March/April 1999 (eiders also occurred at other scattered locations in the wintering area). Once at both stations, we dragged a chain dredge fitted with a canvas liner along the bottom as the ship drifted at about 1 knot (1.85 km/h) for 30 min; this method yielded high sample sizes of clams. Lengths of all *Nuculana radiata*, *M. calcareea*, and *Nucula belloti* collected were measured for comparison with lengths of clams in eider esophagi. Based on laboratory determinations, ash-free dry mass (AFDM, in grams) was estimated from shell length (*L*, in millimeters) by the equations: AFDM = 0.00003  $L^{2.751}$  for *Nuculana radiata* ( $r^2 = 0.91$ ,  $n = 138$ ), AFDM = 0.00002  $L^{2.865}$  for *M. calcareea* ( $r^2 = 0.97$ ,  $n = 151$ ), and AFDM = 0.00001  $L^{3.346}$  for *Nucula belloti* ( $r^2 = 0.81$ ,  $n = 125$ ). Subsamples of these clam species were sorted by length class (see below), oven-dried at 60°C, ground with a mortar and pestle, and combusted in a bomb calorimeter to determine the energy density (including shells) of pooled samples within each length class.

At each of the same two stations, we also took four replicate samples with a van Veen grab (area of each sample was 0.1 m<sup>2</sup>). To be considered at the same station for replicate samples, the ship was allowed to drift no more than 0.5 nautical miles (926 m) away from a station's coordinates determined by GPS (geographical positioning system). These samples were washed over a 0.5-mm sieve, preserved in formalin, and later sorted by species, weighed, and the carbon content estimated from regressions. For all clams of the three major species, shell lengths were measured and AFDM estimated from the above regressions relating AFDM to length. Grabs yielded many fewer clams than the dredge, but measured the biomass of each species per unit area.

Although all eiders containing food were collected at station CD1, for analysis of clam length classes we combined dredge and van Veen grab samples, respectively, from stations CD1 and nearby VNG3.5. For the three major clam species, different length classes

did not differ between stations (all  $P > 0.18$ ) in percentages of numbers or AFDM in dredge samples ( $\chi^2$  tests) or AFDM m<sup>-2</sup> in van Veen grab samples (paired *t*-tests). Pooling yielded much larger samples for different length classes, and reflected prey conditions for eiders moving among widely separated leads in the core use area.

## Results

### Diet versus benthic samples

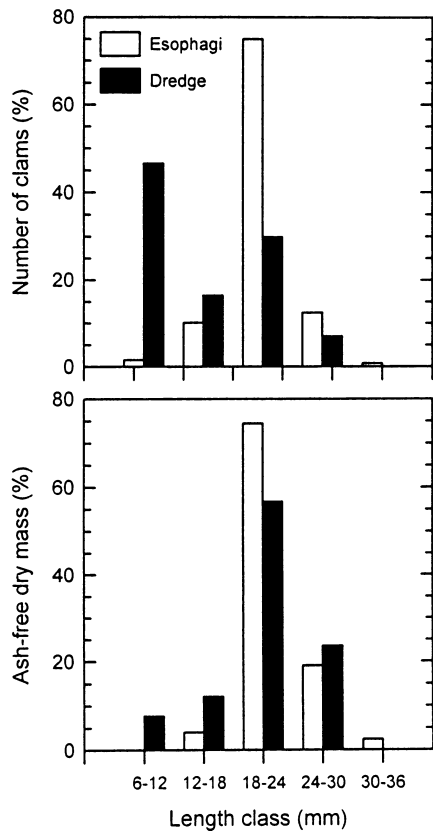
Of the 43 spectacled eiders collected, 12 contained 0.6–32.2 g (mean 10.7 g) dry mass of food in their esophagus (proventriculus). Esophagi of these 12 birds contained 1–58 entire *Nuculana radiata* (total of 221), and 4 birds contained 1–3 entire *Nucula belloti* (total of 8) in addition to *Nuculana radiata*. The aggregate percent dry mass (mean of percentages in each bird) of foods in esophagi was 99.3% *Nuculana radiata* (range 97.0–100%) and 0.7% *Nucula belloti* (range 0–3.0%). Nine of the 12 birds with food in their esophagi also contained 1–9 entire clams (total of 35) in their gizzards, all *Nuculana radiata*. All fragments in esophagi and gizzards were crushed shells of *Nuculana radiata*.

At stations CD1 and VNG3.5, *Nuculana radiata* was very abundant in van Veen grab samples (Table 1). However, prey consumed elsewhere by spectacled eiders (snails, amphipods, other bivalve species; Cottam 1939; Petersen et al. 1998) were also common but not eaten. The rarity of *Nucula belloti* in esophagi and gizzards (<1% dry mass) relative to benthic grab samples at these sites (38–48% of total fresh mass) suggests that the few thick-shelled *Nucula belloti* were ingested incidentally.

Based on dredge samples, which yielded many more clams over a larger area, comparison of numbers eaten versus numbers in benthic samples indicated that eiders selected *Nuculana radiata* 18–24 mm long ( $\chi^2$  test,  $P < 0.001$ , Fig. 2). In terms of AFDM, selection by length class was significant at the 0.1 but not 0.05 level ( $P = 0.098$ ). Eiders ate few, if any, small *Nuculana radiata* despite their high abundance. Lesser numbers and AFDM of *Nuculana radiata* 24–30 mm long were taken about in proportion to their availability (Fig. 2).

**Table 1** Densities of benthic organisms in four van Veen grab samples each at stations CD1 and VNG3.5 (Fig. 1) southwest of St. Lawrence Island in the Bering Sea, 31 March to 1 April 2001. Only taxa comprising >1% of total g C/m<sup>2</sup> (21.54 at CD1, 19.95 at VNG3.5) are included

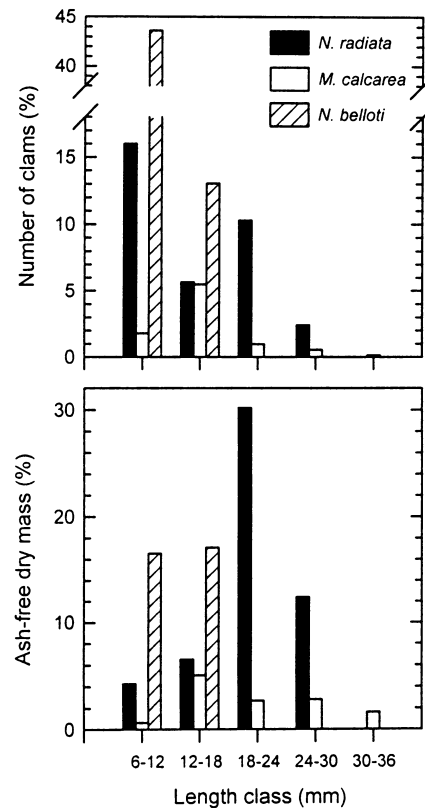
Taxon	Number m <sup>-2</sup>		g C m <sup>-2</sup>		% of total g C	
	CD1	VNG3.5	CD1	VNG3.5	CD1	VNG3.5
Bivalvia						
<i>Nucula belloti</i>	958	1688	12.26	6.69	56.9	33.6
<i>Nuculana radiata</i>	358	1370	3.50	1.44	16.3	7.2
<i>Macoma calcareea</i>	538	263	2.76	2.49	12.8	12.5
Other bivalves	45	213	0.16	0.01	0.8	<0.1
Polychaeta	480	973	2.22	2.78	10.3	13.9
Ophiuridae	28	18	0.46	0.46	2.1	2.3
Amphipoda	85	113	0.07	0.22	0.3	1.1
Gastropoda	125	425	0.03	0.38	0.1	1.9
Rhynchocoela	5	20	0.01	5.45	<0.1	27.3



**Fig. 2** Percentages of numbers and total ash-free dry mass in different length classes of entire *Nuculana radiata* clams in the esophagi and gizzards of 12 spectacled eiders ( $n=256$  clams) collected on 19 March 2001 at station CD1 in the Bering Sea (Fig. 1), and in benthic dredge samples ( $n=2,324$  clams) at stations CD1 and VNG3.5 on 31 March 2001. Relative frequencies differed between esophagus and dredge samples for numbers of clams ( $\chi^2$  test,  $P < 0.001$ ) but not for ash-free dry mass ( $P = 0.098$ )

In dredge samples, when AFDM in different length classes is compared among the three main clam species (Fig. 3), it is clear that most biomass of *Nucula belloti* was in smaller length classes than the biomass of *Nuculana radiata*. Although only 17% of the numbers of *M. calcarea* were in the larger length classes (18–30 mm), 43% of its AFDM was in these same length classes containing *Nuculana radiata* that were commonly consumed by eiders (Figs. 2, 3). Thus, the absence of *M. calcarea* in eider esophagi cannot be attributed to its being too large or too small.

Grab samples yielded lower sample sizes from a smaller area (four 0.1-m<sup>2</sup> replicates per station), but allowed areal measurements. Total AFDMs in grab samples from stations CD1 and VNG3.5 combined were 18.3 g m<sup>-2</sup> for *Nuculana radiata*, 8.8 g m<sup>-2</sup> for *M. calcarea*, and 18.7 g m<sup>-2</sup> for *Nucula belloti*. When AFDM m<sup>-2</sup> is partitioned into length classes (Fig. 4), it again appears that the reason eiders did not eat *Nucula belloti* was not lack of availability, although *Nucula belloti* were smaller than the lengths mostly



**Fig. 3** Numbers and ash-free dry mass in different length classes of the clams *Nuculana radiata* ( $n=2,324$ ), *Macoma calcarea* ( $n=606$ ), and *Nucula belloti* ( $n=3,831$ ), as percentages of totals for all length classes for all three species combined, in dredge samples at stations CD1 and VNG3.5 southwest of St. Lawrence Island in the Bering Sea (Fig. 1) on 31 March 2001

eaten by eiders (18–30 mm, Fig. 2). Although *M. calcarea* was available in these length classes, it had much lower biomass m<sup>-2</sup> than did *Nuculana radiata* (Fig. 4). Moreover, there were many *Nuculana radiata* in smaller length classes that eiders did not eat (Figs. 2, 4).

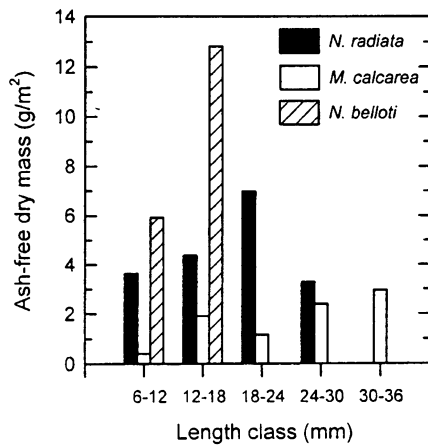
Not all length classes of each clam species were abundant enough to determine energy density (Fig. 3). However, for the same length classes, *M. calcarea* and *Nucula belloti* tended to have higher energy densities (including shells) than did *Nuculana radiata* (Table 2).

#### Body condition

For spectacled eiders in late March 2001 in the Bering Sea, adult males and females did not differ ( $t$ -tests) in protein adjusted for body size ( $P = 0.20$ ) or in total lipid ( $P = 0.12$ ), but females had higher lipid as a percentage of fresh body mass ( $P = 0.008$ ) (Table 3). Sample sizes for juveniles were too low for statistical comparisons; however, values for the three juvenile males were similar to those of adults whereas the two juvenile females had far lower lipid reserves.

**Table 2** Energy density [kJ (g dry mass)<sup>-1</sup> including shells] for different length classes of major clam species south of St. Lawrence Island in the Bering Sea, March/April 2001. Samples were pooled within length class

Length class (mm)	<i>Nuculana radiata</i>	<i>Macoma calcaria</i>	<i>Nucula belloti</i>
6–12	2.663		4.189
12–18	3.508	4.278	4.550
18–24	3.475	5.645	
24–30	3.418	6.324	



**Fig. 4** Ash-free dry mass m<sup>-2</sup> in different length classes of the clams *Nuculana radiata*, *Macoma calcaria*, and *Nucula belloti* in van Veen grab samples pooled for stations CD1 and VNG3.5 southwest of St. Lawrence Island in the Bering Sea (Fig. 1), 31 March to 1 April 2001

## Discussion

### Use of prey types, species, and sizes

On their main wintering area south of St. Lawrence Island, spectacled eiders ate mainly *Nuculana radiata* clams despite availability of other prey used elsewhere

(see below). *Nuculana radiata* was the most abundant acceptable prey. However, its consumption in greater proportion than available, the lack of other prey taken, and selection by length class suggest that eiders developed a specific search image for *Nuculana radiata* 18–24 mm long (cf. Ball 1994). Although *Nucula belloti* were abundant and a few were consumed, the much thicker shell of *Nucula belloti* probably requires more energy to crush in the gizzard. This factor appeared to outweigh the importance of energy content per gram (including shell), which averaged 44% higher in *Nucula belloti* than in *Nuculana radiata* of the same length (6–18 mm). Both *Nuculana radiata* and *Nucula belloti* occur at or very near the sediment surface, whereas *M. calcaria* of comparable size live deeper in the sediments (mostly < 10 cm deep). It is likely that the much lower abundance and deeper burial depth of *M. calcaria*, and the less easily crushed shell of *Nucula belloti*, contributed to predominant use of *Nuculana radiata* by spectacled eiders at this place and time.

Petersen et al. (1998) collected 36 spectacled eiders near the southern shore of St. Lawrence Island. They identified a number of species by fragments and expressed their results as percent occurrence, suggesting that their samples came from both the glandular stomach or proventriculus and the muscular stomach or gizzard (Swanson and Bartonek 1970; Welty and Baptista 1988). Sediments near the island where those birds were collected are much sandier than in the main wintering area 60–145 km to the southwest, and the benthic community is correspondingly different (Grebmeier and Cooper 1995). Percent occurrence of foods in eiders was 80% for bivalves, 31% for crustaceans, and 20% for snails. In 36% of samples, three species of *Macoma* were the only food; in 12% of samples *M. calcaria* was the sole taxon, and in 11% of samples *Chionoecetes* spp. crabs were the only food. Prey items included two species of snails, four genera of clams, two species of amphipods, and four genera of crabs, barnacles, and cod. In another report (Cottam 1939), two spectacled eiders from the Pribilof Islands, Alaska contained 90% amphipods and some snails. Although prey availability was

**Table 3** Mean ( $\pm$ SD) fresh bodymass (including feathers), composition of the sheared body, and percent lipid in fresh body mass of spectacled eiders collected southwest of St. Lawrence Island in the Bering Sea, 19 April 1999 (1 adult male) and 19–22 March 2001 (all others). Ranges of values are in parentheses

		Fresh body				Adjusted		
		Mass (g)	Water (g)	Ash (g)	Protein (g)	Protein (g)	Lipid (g)	% lipid in fresh mass
Adult male	26	1688 $\pm$ 109 (1469–1956)	1032 $\pm$ 45 (956–1145)	69 $\pm$ 12 (45–97)	386 $\pm$ 25 (346–454)	374 $\pm$ 22 (334–429)	200 $\pm$ 58 (75–299)	11.7 $\pm$ 2.9 (5.1–16.5)
Juvenile male	3	1488 $\pm$ 39 (1445–1522)	908 $\pm$ 27 (891–940)	59 $\pm$ 11 (51–71)	346 $\pm$ 2 (344–348)	351 $\pm$ 30 (317–372)	186 $\pm$ 35 (158–225)	12.5 $\pm$ 2.2 (11.0–15.0)
Adult female	12	1550 $\pm$ 120 <sup>a</sup> (1272–1789)	919 $\pm$ 58 <sup>a</sup> (840–1044)	62 $\pm$ 10 (44–79)	350 $\pm$ 28 <sup>a</sup> (314–396)	367 $\pm$ 25 (341–429)	224 $\pm$ 55 (83–310)	14.3 $\pm$ 3.0 <sup>a</sup> (6.5–17.3)
Juvenile female	2	1216 $\pm$ 57 (1176–1257)	794 $\pm$ 48 (760–828)	55 $\pm$ 24 (38–72)	300 $\pm$ 16 (289–311)	356 $\pm$ 3 (353–358)	69 $\pm$ 19 (55–82)	5.7 $\pm$ 1.8 (4.4–7.0)

<sup>a</sup>Higher than in males (*t*-test,  $P < 0.008$ , tests for adults only)

not measured, these data show that spectacled eiders consume a wide variety of prey under different circumstances. This flexibility highlights the apparent selection of *Nuculana radiata* by birds on the main wintering area, while *M. calcareea* and other viable prey were present but in lower mass.

*Nuculana radiata* eaten by spectacled eiders were of intermediate length (Fig. 2). Several studies have shown size selection of bivalves by diving ducks and especially common eiders eating mussels (Draulans 1982, 1984; Bustnes and Erikstad 1990; de Leeuw and van Eerden 1992; Bustnes 1998; Guillemette 1998; Hamilton et al. 1999). Size selection has been explained by differential handling times, effects of meat:shell ratios on nutrient gain relative to passage rates, or as a means of avoiding the risk of ingesting prey that are too large. For *Nuculana radiata*, *M. calcareea*, and *Nucula belloti*, neither meat:shell ratios nor nutrient content relative to ash change consistently with length (S.E. Richman and J.R. Lovvorn, unpublished data). In our large sample of thin-shelled clams (*Nuculana radiata*, *M. calcareea*), few individuals were too large to be easily swallowed or crushed by spectacled eiders (Fig. 3). Thus, eiders probably consumed *Nuculana radiata* of intermediate length because most of its biomass was in that range, and because energy intake per unit handling time was greater than for smaller clams.

From the early 1960s to the late 1980s, dominance of benthic biomass in this area is thought to have shifted from *M. calcareea* to *Nuculana radiata* (Sirenko and Koltun 1992; National Research Council 1996). In March/April 2001, large samples from the dredge indicated that the biomass of *M. calcareea* was far lower than for *Nuculana radiata* (Fig. 3), and this difference appears to be the main reason that eiders ate mainly *Nuculana radiata*. Compared to *Nucula radiata* of the same length, energy per gram dry mass (including shell) was 62% higher in *M. calcareea* 18–24 mm long (5.645 vs 3.475 kJ), and 85% higher in *M. calcareea* 24–30 mm long (6.324 vs 3.418 kJ). This difference might be somewhat offset by the shallower burial depth and thus greater accessibility of *Nuculana radiata*. However, the long-term decrease in energy density of the dominant prey in this area may have appreciably affected the profitability of diving 40–70 m to feed.

### Body condition

For adult spectacled eiders near the end of winter, percent lipid in total body mass averaged 11.7% in males and 14.3% in females. These percentages are similar to those of adult canvasbacks (*Aythya valisineria*) near the end of winter in North Carolina (males 12.0%, females 12.2%; Lovvorn 1994), but lower than in Louisiana where conditions are more benign (combined sexes 19.0%; Hohman 1993). Canvasbacks gain substantial fat toward the end of spring migration before arrival at nesting areas (Barzen 1989), and acquiring prebreeding

reserves appears critical for canvasbacks which draw heavily on stored lipid for egg-laying and incubation (Barzen and Serie 1990). Although few data are available for spectacled eiders, common eiders are known to depend heavily on stored reserves during egg-laying and incubation, when they eat little if at all (Korschgen 1977; Parker and Holm 1990; Erikstad et al. 1993). Clutch size, nest success, brood attendance by hens, and resulting survival of ducklings also depend on adequate prebreeding reserves (Bustnes and Erikstad 1991; Erikstad et al. 1993; Bustnes et al. 2002; Oosterhuis and van Dijk 2002). Feeding conditions on areas used before arrival at nesting sites appear critical to prebreeding reserves (Pehrsson 1975; Milne 1976; Parker and Holm 1990; Christensen 2000; Guillemette 2001), and many common eider females do not nest in years when feeding conditions on such areas are poor (Coulson 1984; Oosterhuis and van Dijk 2002).

Studies of spectacled eiders have not revealed clear relationships between the body mass and incubation constancy of different individuals (Flint and Grand 1999). However, spectacled eider females on the Y-K Delta lost 530 g from arrival at nesting areas to the time of hatching, and their weights stayed depressed for at least 30 days after that (Petersen et al. 2000). This pattern suggests that nest success and brood attendance depend strongly on prebreeding reserves, as in common eiders. Body mass (mean  $\pm$  SE, range) of our 26 males in late March (1,688  $\pm$  21 g, 1,469–1,956) was substantially higher (*t*-test,  $P < 0.001$ ) than reported for 53 males soon after arrival at the Y-K Delta in late May (1,494  $\pm$  14 g, 1,275–1,750), whereas the body mass of 12 adult females in late March (1,550  $\pm$  35, 1,272–1,789) did not differ (*t*-test,  $P = 0.110$ ) from that reported for 11 adult females (1,623  $\pm$  46, 1,300–1,850) upon arrival at the Y-K Delta (Petersen et al. 2000). On the Y-K Delta, as many as 90% of spectacled eiders arrive during a period of 3–4 days in the 2nd or 3rd week of May, when no nest sites are available owing to flooding by meltwater; however, nearly 80% of nests have been initiated by the end of the 1st week in June (Dau 1974). With minimal time for feeding between arrival and egg-laying, it appears that females acquire prebreeding reserves mainly in marine habitats before arrival at nesting sites.

### Spring habitat, climate, and seaduck populations

In 1999, over 10 h of searching by helicopter from 22 to 26 April indicated that the last spectacled eiders on the wintering area left on 21 April, when many eiders were seen flying north. Given the importance of foraging habitats during spring migration, where do spectacled eiders go during the 4–6 weeks between leaving the wintering area and arriving at breeding sites on the Y-K Delta, or the 6–8 weeks before arriving at sites in northern Siberia (Pearce et al. 1998)? Although they may congregate nearer the southern shore of St. Lawrence Island in October/December (Petersen et al. 1999),

helicopter flights revealed no eiders there after they disappeared from the main wintering area to the southwest in April 1999. Many spectacled eiders approach their breeding areas on the Y-K Delta from the north, suggesting the existence of spring staging areas north of St. Lawrence Island (McCaffery et al. 1999).

In April 1999, all eiders departed the wintering area when the prevailing northerly winds shifted to the south; such a change would also shift the polynya and associated leads from south to north of St. Lawrence Island (Niebauer et al. 1999). In that area of the Chirikov Basin, the water is about half as deep (15–25 m) as in the wintering area, and benthic densities are also quite high, although dominance often changes from bivalves to amphipods (Grebmeier 1993; Grebmeier and Cooper 1995; Grebmeier and Dunton 2000). The Chirikov Basin benthos may be experiencing declines and changes in community structure owing to heavy feeding by the growing population of gray whales (*Eschrichtius robustus*), as well as invasion by other predators during long-term climate warming (Highsmith and Coyle 1992; Coyle and Highsmith 1994).

It is likely that eiders breeding in Siberia and on the North Slope eventually move closer to nesting areas via polynyas and leads that form during spring in the same locations from year to year (Stirling 1980; Prach et al. 1981; Alexander et al. 1997; Solovieva 1999). The drawback to such areas is that when severe weather closes these lead systems unexpectedly, catastrophic mortality of eiders can occur. For example, an estimated 100,000 king eiders (*S. spectabilis*) died when a major lead system along the Beaufort Sea coast closed in mid-May 1968; a number of similar events have been recorded as recently as 1990 (Barry 1968; Palmer 1976; Fournier and Hines 1994). Such losses could have important impacts on spectacled eiders, and on western populations of king eiders, common eiders, and long-tailed ducks (*Clangula hyemalis*) that use such habitats and have shown declines of 50–90% (Prach et al. 1981; Hodges et al. 1996; Dickson et al. 1997; Solovieva 1999; Suydam et al. 2000). These patterns suggest that dramatic fluctuations in seaduck numbers at high latitudes may not be unusual, at least partly because of the effects of variable ice conditions on foraging opportunities in the spring.

Habitats used to acquire prebreeding reserves appear critical to spectacled eiders, because unpredictable ice conditions place a premium on alternative habitats. Thus, it is important to determine habitat use and body condition of females during spring migration, and how body condition affects the fraction of females that attempt to breed and their subsequent success. Also, studies are needed to evaluate and predict how altered availability of *Nuculana radiata*, *M. calcareo*, and other prey affect the energy balance of eiders. With climate-related changes in the Bering Sea, shifts in prey communities, weather, and ice dynamics may have important impacts on spectacled eiders and other seaducks.

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