

Effects of clam species dominance on nutrient and energy acquisition by spectacled eiders in the Bering Sea

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ABSTRACT: The spectacled eider *Somateria fischeri*, a 'threatened' species, winters in pack ice of the Bering Sea. In dives of 40 to 70 m for benthic invertebrates, the high energy costs of foraging are offset by high benthic biomass. However, there is evidence that the dominant clam prey has changed from *Macoma calcareo* to *Nuculana radiata*, perhaps adversely affecting the foraging energetics of the eiders. We studied effects of differences in nutrient and energy content, crushing resistance of shells, digestibility, gut retention time, areal density, shell length, and depth in the sediments on the relative foraging value of *M. calcareo* versus *N. radiata*. To avoid using a 'threatened' species for experiments, we used common eiders *Somateria mollissima* for digestion studies and white-winged scoters *Melanitta fusca* (the same size as spectacled eiders) for foraging studies. For the prey size range comprising 93% of the eiders' diet (18 to 30 mm), *M. calcareo* including shells was lower in ash, and higher in nitrogen, lipid, and energy, than *N. radiata*. Digestibility was 76% for *M. calcareo* versus 67% for *N. radiata*, but gut retention time did not differ. In a tensometer, crushing resistance was much higher for *N. radiata* than *M. calcareo* for shells 18 to 24 mm long, but did not differ for 24 to 30 mm because shells of *N. radiata* were often severely abraded. For scoters foraging on freshly thawed *Macoma balthica* buried in sand in an aquarium 1.8 m deep, intake (no. s⁻¹) decreased by 31% when burial depth in the sediments was increased from 4 to 7 cm; most *N. radiata* are <4 cm deep, and most *M. balthica* eaten by eiders are probably 7 to 10 cm deep. Considering energy content, digestibility, and intake rates at these burial depths for 1200 clams m⁻², energy assimilated was 14 to 19% higher for *N. radiata* than *M. calcareo* of the same length classes. However, larger *M. calcareo* yielded 58% higher intake of assimilable energy than smaller *N. radiata*. These patterns emphasize that relative foraging value depends strongly on size (age) structures of different prey populations, which vary with recruitment, growth, and mortality in different seasons and years. Our results show that impacts of long-term benthic change on eiders depend not only on shifts in total clam abundance, but also on species differences in digestibility, size structure, and size-dependent nutrient content and burial depth.

KEY WORDS: Spectacled eider · Foraging energetics · Bering Sea · Food intake rate · Functional response · Digestibility · Retention time · Sea duck

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INTRODUCTION

From the early 1970s to the early 1990s, spectacled eiders *Somateria fischeri* nesting on the Yukon-Kuskokwim (Y-K) Delta, Alaska, declined by 96% from 48 000 to 2000 pairs, apparently stabilizing at that low level (Stehn et al. 1993, Ely et al. 1994, Petersen et al.

2000). At the 2 other main nesting areas, trends on the north coast of Siberia (~90% of all current breeders) are unknown (Petersen et al. 2000), while numbers on the North Slope of Alaska (~5% of all breeders) from 1992 to 2002 were roughly stable (W. Larned et al. unpubl. data). Based on trends in the Y-K Delta, these eiders were listed as 'threatened' under the US Endan-

gered Species Act in 1993. Reasons for the decline are unclear, but modeling indicates that a major limiting factor is adult mortality (US Fish & Wildlife Service 1996). Lead poisoning causes appreciable mortality of adult females during breeding, but up to 46% of the annual mortality of adult females there appears to occur in the non-breeding period when the eiders are at sea (Grand et al. 1998, Flint et al. 2000). From late December to mid-April, the only known wintering area for spectacled eiders is among leads in the pack ice of the Bering Sea southwest of St. Lawrence Island (Petersen et al. 2000). There they dive 40 to 70 m for benthic prey, mainly bivalves, which have been present in very high densities (Grebmeier & Cooper 1995, Grebmeier & Dunton 2000, Lovvorn et al. 2003).

In the Bering Sea, an oceanic regime shift to warmer conditions occurred in 1976–77, and apparently a lesser shift (still with warm temperatures) in 1989 (Hare & Mantua 2000, Bond & Adams 2002). These shifts caused widespread alterations in the Bering Sea food web (National Research Council 1996, Connors et al. 2002, Hunt et al. 2002). Perhaps as part of this change, *Macoma calcaria*, which dominated clam biomass in the 1950s and early 1960s, had been replaced in dominance by the clam *Nuculana radiata* by the late 1980s (Sirenko & Koltun 1992, National Research Council 1996). Studies begun in the mid-1980s have shown declines in the biomass m^{-2} and mean sizes of clams (Grebmeier & Dunton 2000). In areas where the eiders winter, the bivalve community now consists mainly of *N. radiata* and *Nucula belloti*, with much lower abundance of *M. calcaria* (National Research Council 1996). Over 99% of the dry mass eaten by 12 spectacled eiders collected on the wintering area in March 2001 was *N. radiata*, with no *Macoma calcaria* and only traces of *N. belloti* (Lovvorn et al. 2003). Although this sample of eiders was small and from a limited area, it indicates that *N. radiata* dominates the current diet of spectacled eiders in their main wintering habitat.

Details of the chronology and spatial extent of the benthic shift are unknown; however, available data raise questions about effects on the foraging energetics of eiders, and their acquisition of body reserves for overwinter survival and reproduction (Lovvorn et al. 2003). In common eiders *Somateria mollissima*, adequate fat stores in females are important to both nest success and duckling survival (Korschgen 1977, Bustnes & Erikstad 1991, Erikstad et al. 1993, Swennen et al. 1993), and many females do not nest in years when their body reserves are too low (Coulson 1984). Prey conditions before arrival at nesting sites appear to be critical for acquiring the needed reserves (Pehrsson 1975, Milne 1976, Parker & Holm 1990, Christensen 2000, Guillemette 2001, Oosterhuis & van Dijk 2002). For spectacled eiders, a shift in dominant prey species

on wintering areas, together with decreased density and size of clams (Grebmeier & Dunton 2000), might have played a role in population trends.

Acquisition of nutrients and energy depends on the intake rate of food items, and the food's size, nutrient content, digestibility, and retention time in the gut (Kaiser et al. 1992, Ball 1994, Jeschke et al. 2002). Rate of food intake at a range of prey densities, known as the functional response, is critical to foraging profitability (energy gain minus cost) (Myers et al. 1980, Wanink & Zwarts 1985, Draulans 1987, Piersma et al. 1995). A type 2 functional response, in which intake rate increases with increasing prey density up to an asymptote where intake is limited by handling time, often typifies diving duck foraging on benthic foods (Giles 1990, Lovvorn & Gillingham 1996). Prey depth in the sediments has important effects on the functional responses of crabs and shorebirds eating clams (Wanink & Zwarts 1985, Lipcius & Hines 1986, Zwarts & Blomert 1992, Seitz et al. 2001), but effects of prey depth have seldom been studied for diving ducks (Carbone 1995, Richman 2002). Nutrient and energy content, digestibility, and crushing resistance of shells can vary with both species and size of bivalves (Beukema & de Bruin 1977, Jorde & Owen 1988, Bustnes & Erikstad 1990, Piersma et al. 1993), and various studies have shown size selection of bivalves by diving ducks (Draulans 1982, 1984, Bustnes & Erikstad 1990, de Leeuw & van Eerden 1992, Bustnes 1998, Hamilton et al. 1999). In these studies, preference for smaller bivalves than expected was explained by differential availability, handling times, effects of meat:shell ratios on nutrient gain relative to passage rates, or as a means of avoiding prey that are too large to swallow. Resistance of shells to crushing in the gizzard may also affect selection of species and sizes of bivalve prey (Navarro et al. 1989).

For the clams *Nuculana radiata*, *Macoma calcaria*, and *Nucula belloti*, we measured the energy and macronutrient content and crushing resistance of shells. Because *N. belloti* was eaten in only trace amounts (Lovvorn et al. 2003), we measured the digestibility and gut retention time by captive eiders of *N. radiata* and *M. calcaria* only. We also determined the functional responses of ducks foraging on freshly-thawed clams of different sizes buried at different depths in sand at the bottom of an aquarium. To avoid using a 'threatened' species in experiments, we used common eiders for digestion studies, and white-winged scoters *Melanitta fusca* (the same size as spectacled eiders) for studies in the dive tank. Applicability of results for scoters was verified by trials with a captive spectacled eider.

Given the high densities achieved by these clams in the field, we carried out repeated foraging experi-

ments at densities up to 1600 m⁻². To collect so many clams of suitable size during cruises in the Bering Sea was impractical, so instead we used *Macoma balthica* collected with a commercial clam dredge in Chesapeake Bay, Maryland, USA. Results for *M. balthica* were assumed to be the same as for *M. calcareea*, and their applicability to *Nuculana radiata* was confirmed by a set of trials with the latter species. The specially designed dive tank we used (see 'Materials and methods') was in prairie Canada, and it was infeasible to transport and maintain such large numbers of live salt-water clams (~30 000 *M. balthica* and 4000 *N. radiata*) for several months of experiments in this freshwater tank. In the field, burial depths of clams can increase during winter when birds are present; however, such trends appear to be long-term and driven by cohort age or seasonal physicochemical factors, rather than short-term predator avoidance per se (Reading & McGroarty 1978, Evans 1979, Zwarts et al. 1992). Experiments have shown that subtidal clams do not alter their behavior during close approach by isopod or fish predators (Peterson & Quammen 1982, Peterson & Skilleter 1994, Tallqvist 2001), and measured burrowing rates of 0.07 to 0.13 mm s⁻¹ in either sand or mud (Stanley 1970, Tallqvist 2001) are far too slow to avoid capture after detection by diving ducks. Because ducks consume whole clams rather than just nipping their siphons (cf. Skilleter & Peterson 1994), retracting siphons would not prevent ingestion by ducks. Thus, predation rates on freshly-thawed clams should be reasonably similar to those on live clams.

By combining data on functional responses and clam composition and digestibility, we compared *Nuculana radiata* and *Macoma calcareea* in terms of their foraging value (intake rate of digestible nutrients at a given prey density). This comparison provided insights into possible effects of a shift in clam species dominance on the foraging energetics of spectacled eiders during winter.

MATERIALS AND METHODS

Composition and crushing resistance of clams.

Shell lengths of *Nuculana radiata*, *Macoma calcareea*, and *Nucula belloti* collected in the Bering Sea (Stns CD1 and VNG3.5, see Lovvorn et al. 2003) were measured along the anterior-posterior axis to the nearest 0.1 mm, and divided into 6 mm length classes (6.1 to 12.0 mm, 12.1 to 18.0 mm, 18.1 to 24.0 mm, and 24.1 to 30.0 mm). Soft tissues of individual clams were dissected from the shell, and soft tissues, shells, and whole clams (separate samples) were weighed to the nearest 0.0001 g and oven-dried separately at 60°C to constant mass. Water content and dry mass of shell,

soft tissue, and whole clams were averaged for each length class. Individual shells and soft tissue were burned in a muffle furnace at 500°C for 6 h to yield ash-free dry mass (AFDM). Ash mass of soft tissue was negligible and not included in calculating AFDM. These data were fitted with nonlinear regressions. Uneven distributions of samples along a rising curve within a length class could bias the mean value for that length class. Consequently, we used predicted values at the midpoint of each length class, and considered these values to differ between length classes if their 95% confidence intervals did not overlap.

Energy analyses with bomb calorimetry required larger samples (~0.5 g dry mass including shell) than were contained in most individual clams (see 'Results'). Therefore, we pooled 5 whole clams for each species and length class, except for the 6 to 12 mm length class, for which 10 clams of each species were pooled. Nitrogen and lipid analyses were performed on flesh removed from shells. Lipid content, determined by extraction with petroleum ether, again required more material than was contained in single clams, so 10 clams were pooled for each species and length class. Subsamples of the dried flesh homogenate were analyzed for nitrogen content with an elemental analyzer (Fison Instruments). Fractions of energy, lipid, and nitrogen for pooled samples were then converted to absolute amounts for the mean dry mass of each species and length class.

Because eiders consume whole clams and crush the shells in their gizzard, we used a tensometer (Soiltest) to measure the force needed to crack the shells of each bivalve species in different length classes. The pressing surfaces contacted opposing valves just below the umbo (thickest part of the shell). Force was gradually increased until the shell first cracked.

Digestibility trials. Feeding trials were conducted from November to December 2000 at the University of Wyoming. Two common eiders were raised from eggs collected on Pancake Island, Nova Scotia, Canada, in June 2000, and 2 males and 2 females were obtained from a private aviculturist. When not involved in feeding trials, the eiders were housed in an outdoor aviary and fed a diet of 2 parts Mazuri® Waterfowl Maintenance (14.0% crude protein, 3.0% crude fat, 4.5% crude fiber) to 1 part Mazuri® Sea Duck Diet (21.5% crude protein, 5.0% crude fat, 4.5% crude fiber). Grit was not supplied for 2 wk before and during the trials, to prevent variability due to grit in excreta mass and nutrient analyses.

Nuculana radiata and *Macoma calcareea* were collected south of St. Lawrence Island in the Bering Sea and stored frozen until thawed before experiments. Shell lengths of clams fed to the birds corresponded to lengths eaten by spectacled eiders in the Bering Sea

(12 to 30 mm, Fig. 1). Common eiders were placed in individual metabolism cages (61 × 45 × 33 cm) with galvanized metal sides, and with wire mesh flooring through which excreta dropped onto collection trays lined with plastic sheets. Water was provided ad libitum throughout the experiments. Feeding trials consisted of (1) a 24 h period of acclimation to the cages, (2) a 24 h fasting period, (3) a single force-feeding of a known mass of clams (about 35 g fresh mass including shells), and (4) a 48 h excreta collection period. Each bird was used in 2 feeding trials, in which 1 group of 3 eiders was fed *M. calcareea* in the first trial and then *N. radiata* in the second trial, and the second group of 3 eiders was fed in the reverse order. Two eiders did not adjust well to experimental conditions during the trial feeding of *N. radiata*, showing behavioral stress and anomalous defecation patterns; these birds were removed from analyses. *Nucula belloti* was not used in digestibility trials because it was eaten in only trace amounts, appar-

ently incidentally, by spectacled eiders collected in the study area (Lovvorn et al. 2003). These eiders had also eaten no *M. calcareea*; however, *Macoma* spp. were the most common food, while *N. radiata* and *N. belloti* were absent, in esophagi and gizzards of spectacled eiders collected in nearshore areas of St. Lawrence Island from 1987 to 1995 (Petersen et al. 1998).

The test diet was force-fed to the birds by opening the bill and placing thawed clams at the back of the throat with tweezers. Birds were allowed to swallow, but if clams became lodged in the esophagus, a Tygon tube (25 cm long and 2 cm wide) was inserted into the throat, pulled back to the top of the proventriculus, and flushed with distilled water from a squeeze bottle. This method of intubation has often been used in digestibility studies with chickens (Sibbald 1979), ducks (Jorde & Owen 1988), and seabirds (Kirkwood & Robertson 1997). Eiders were weighed at the beginning of the acclimation period, immediately before feeding, and at the end of the trial.

During the 24 h fasting period, endogenous excreta were collected every 4 h. After feeding the test diet, excreta were collected hourly for the first 24 h and every 2 h for another 24 h. Ambient temperature was maintained at 13 to 15°C with natural photoperiod (10:14 L:D). Because birds excrete both feces and excretory waste (collectively termed excreta) through a common cloaca, samples were collected and analyzed together. Excreta were transferred to a plastic urine cup with a rubber-coated spatula or pipette, and frozen until analyzed. Excreta were later oven-dried at 60°C to constant mass, and subsamples were ground and homogenized. Content of energy, lipid, nitrogen, and ash were measured as described above.

Assimilation efficiency (*AE*), or metabolizable energy coefficient, is the fraction of food ingested that is absorbed by the gut. Apparent assimilation efficiency was calculated for each bird fed each clam species by the formula

$$AE = (GE_{in} - GE_{out})/GE_{in} \quad (1)$$

where GE_{in} and GE_{out} are gross energy ingested and excreted (in kJ). Assimilated energy was corrected for nitrogen balance (*NB*, in kJ) by the formula (Brekke & Gabrielsen 1994)

$$AE_N = [GE_{in} - (GE_{out} + NB)]/GE_{in} \quad (2)$$

where

$$NB = (N_{in} - N_{out}) \times 36.5 \quad (3)$$

In Eq. (3), N_{in} and N_{out} are nitrogen ingested and excreted (g), and 36.5 is the mean energy content (kJ) per gram urine-nitrogen in birds (Titus et al. 1959, Sibbald 1982). Correction for nitrogen balance is needed because the energy in excreta from endogenous

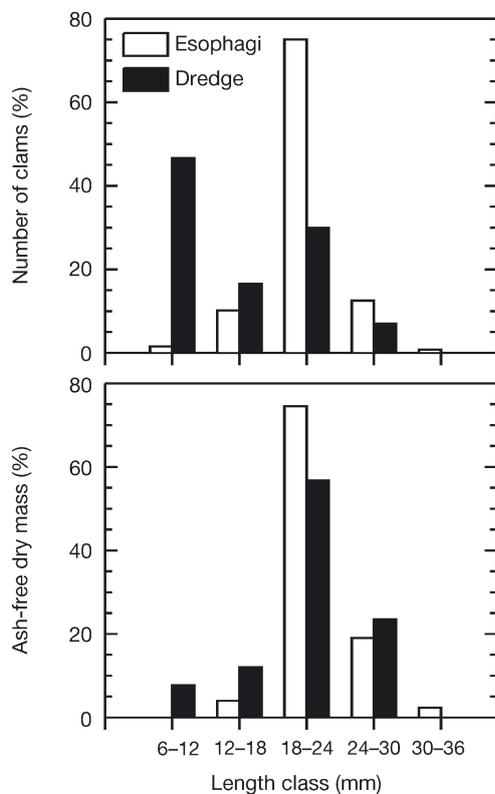


Fig. 1. *Nuculana radiata*. Percentages of numbers and of total ash-free dry mass (AFDM) in different length classes of entire *N. radiata* clams in the esophagi of 12 spectacled eiders ($n = 256$ clams) collected on 19 March 2001 in the Bering Sea, and in benthic dredge samples ($n = 2324$ clams) near the eider collection site on 31 March 2001. Over 99% of dry mass consumed by these eiders was *N. radiata*. Relative frequencies differed between esophagus and dredge samples for numbers of clams (χ^2 test, $p < 0.001$) but not for AFDM ($p = 0.098$). Data: Lovvorn et al. (2003)

sources (e.g. protein breakdown products, gut epithelial cells, enzymes) can otherwise result in underestimates of assimilation efficiency.

Gut retention time. The time required to process food in the gut can be longer than the time needed to find, handle, and ingest food (Jeschke et al. 2002). If the sum of digestive processing time and foraging time exceeds the time available for foraging, differences among prey in gut retention time can affect acquisition of nutrients and energy (Guillemette 1994, 1998). Mean retention time (*MRT*) in the gut from mouth to anus was calculated as

$$MRT = \frac{\sum_{i=1}^n E_i t_i}{\sum_{i=1}^n E_i} \quad (4)$$

where E_i is the mass of excreta produced during the collection period i , t_i is time since the trial feeding, and n is the number of collections (Jackson 1992, Hilton et al. 2000). Absolute values of *MRT* can depend on how long sampling is continued beyond the time when most of a meal has been excreted (Hilton et al. 1998). To ensure that this variation did not affect tests between *Nuculana radiata* and *Macoma calcarea*, *MRT* was compared between species for total collection durations of 12, 18, and 24 h after feeding.

Functional responses. Foraging studies were conducted at the Delta Waterfowl and Wetlands Research Station (DWWRS), Manitoba, Canada, in a large concrete tank (2 × 5 × 2 m deep). Water depth was 1.8 m. Plate glass windows in walls of the tank allowed observations and video filming of the ducks underwater. To avoid using a 'threatened' species for all experiments, white-winged scoters, which are similar to eiders in body mass and foraging behaviors, were used as a proxy for spectacled eiders. Scoters were collected as eggs at Redberry Lake Reserve near Hafford, Saskatchewan, and raised at the DWWRS; these birds were either 1 or 2 yr old during foraging trials. We obtained nine 1 yr old spectacled eiders from a private aviculturist to validate the relevance of results from scoters; however, only 1 of these birds would dive by itself consistently to allow measurements of intake rate. The ducks were acclimated to the dive tank and allowed to dive and feed in a sand-filled tray (0.5 m wide × 1 m long × 9 cm deep) at the bottom of the tank for at least 2 wk before experiments started.

Four scoters (2 of each sex) foraged for 2 length classes of clams (18.1 to 24.0 mm and 24.1 to 30.0 mm) at 7 densities from 50 to 1600 m⁻², at 2 depths in the sand (4 and 7 cm). For such extensive experiments, collecting enough clams during cruises in the Bering Sea was impractical. Consequently, we used *Macoma balthica*, a similar congener of *M. calcarea*, collected with a commercial clam dredge in Chesapeake Bay, Maryland, USA. The clams were frozen until thawed before exper-

iments. To verify that intake rates of spectacled eiders were the same as for white-winged scoters, we did comparative trials with 1 captive-reared female spectacled eider. For all experiments, prey densities were presented in random order to randomly selected birds.

Freshly thawed clams were counted and uniformly distributed on the bottom of the tray. The clams were then covered with clean sand to a depth of 4 or 7 cm, depending on the trial. Sand depth (and thus burial depth of clams) was established with wooden scrapers constructed to create depths of 4 or 7 cm above the bottom of the tray. The tray was lowered to the bottom of the dive tank and raised after the trial with a winch. After the foraging bout, the remaining clams were counted after washing the sand through a 2 mm mesh screen. Number of clams consumed was calculated by subtraction. Time spent foraging at the bottom (probing the sand) was measured from video films as the time between the bill entering and exiting the sand. To prevent a large decrease in prey density, trials were terminated when the bird was estimated to have consumed no more than 10% of available prey, based on typical intake rates while probing the sand.

Intake rates of scoters feeding on *Macoma balthica* were fitted with Michaelis-Menten equations (Marquardt method, PROC NLIN, SAS Institute 1987). In the equation, $I = aX/(b + X)$, I is the number of clams consumed per second at the bottom, X is the number of clams m⁻², a is the handling time coefficient or the maximum rate at which clams can be consumed regardless of clam density, and b is the search time coefficient or the clam density at an intake rate of $0.5a$ (Lovvorn & Gillingham 1996).

Note that recent functional response models that account for satiation effects (Jeschke et al. 2002) are not appropriate for our application, in which intake during a single dive rarely achieves satiation (filling of the esophagus-proventriculus). Dive bouts alternate cyclically with preening and resting periods (Guillemette 1994). Because of the high energy cost of diving (de Leeuw 1996, Kaseloo 2002), intake rate should be maximized during each dive to minimize time underwater, with bouts of a series of dives simply being terminated upon satiation (Lovvorn & Gillingham 1996). Digestion appears to occur mainly during a resting period after the dive bout, when costs of floating on the water surface are far less than during dives (Kaseloo 2002).

Differences between functional response curves were tested with *F*-statistics comparing residual errors from combined versus separate models (Chatterjee et al. 2000). To compare curves based on multiple white-winged scoters eating *Macoma balthica* to curves from a single scoter eating *Nuculana radiata* or a single spectacled eider eating *M. balthica*, we used *t*-tests on the slopes of log-transformed functional responses.

RESULTS

Composition and crushing resistance of clams

For all 3 clam species, dry mass, ash mass, and AFDM increased nonlinearly with increasing shell length (Fig. 2). In the main length classes eaten by spectacled eiders collected in the study area (12 to 30 mm, Fig. 1), *Nucula belloti* contained 59% more ash than *Nuculana radiata* and almost 3 times more than *Macoma calcaria* (Table 1). *N. radiata*

contained 32 to 80% more ash than *M. calcaria*. Meat content (AFDM) was the same for *N. radiata* and *M. calcaria* 12 to 24 mm long, but was 17% higher in *M. calcaria* 24 to 30 mm long. Despite its much greater ash content, *N. belloti* had AFDM over twice that of the other species for clams 12 to 18 mm long.

In most length classes, nitrogen content was 6 to 19% higher, and lipid content 51 to 68% higher, in *Macoma calcaria* than in *Nuculana radiata* (Table 2). In small clams (12 to 18 mm), energy content was 26%

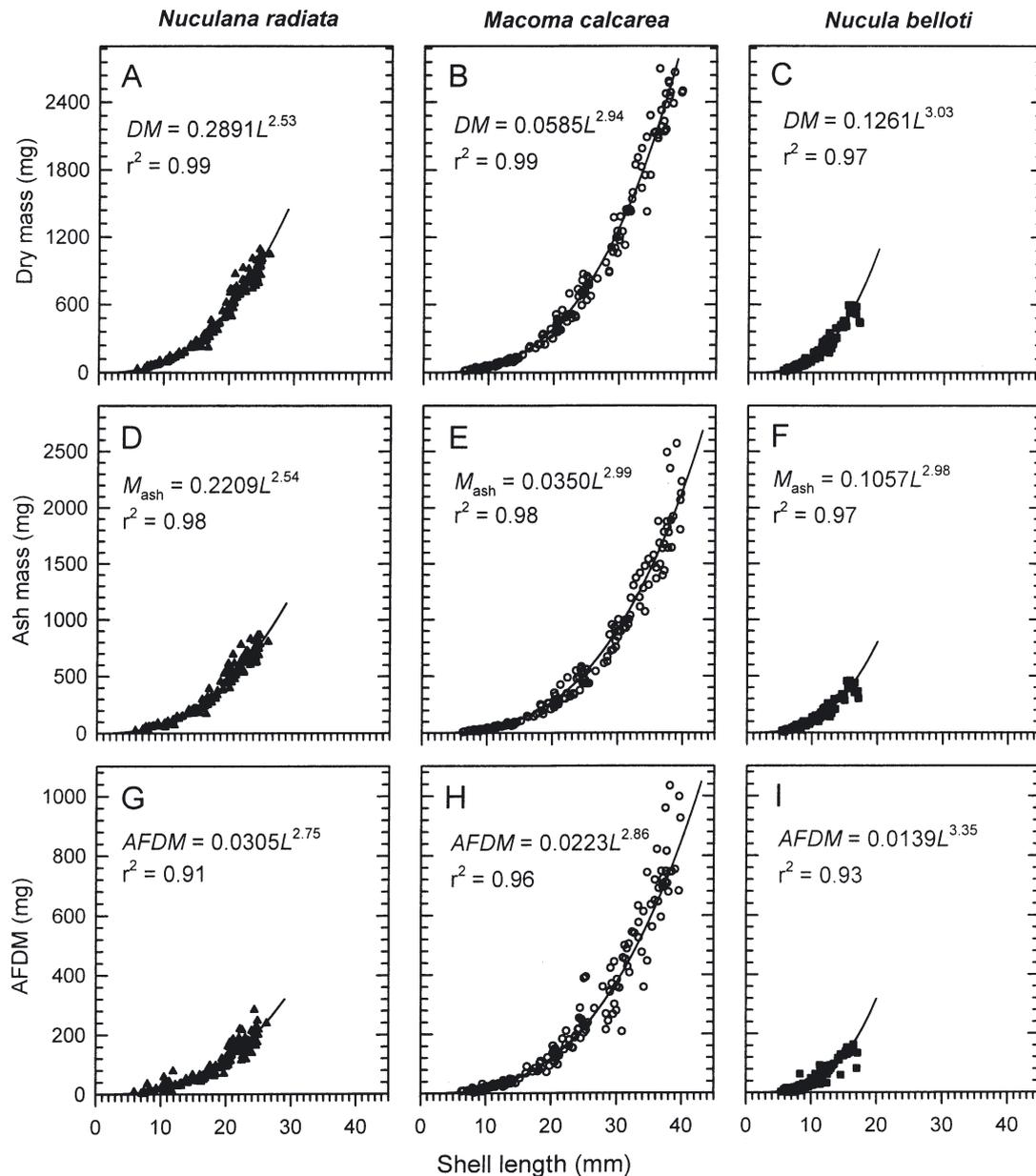


Fig. 2. *Nuculana radiata*, *Macoma calcaria*, and *Nucula belloti*. Dry mass (DM), ash mass (M_{ash}), and ash-free dry mass (AFDM) of clams (including shell) from the Bering Sea. $p < 0.001$ for all regressions

Table 1. *Nuculana radiata*, *Macoma calcaria*, and *Nucula belloti*. Predicted values and 95% confidence intervals (CI) from regressions (see Fig. 2) for dry mass, ash mass, and ash-free dry mass (AFDM) per clam (including shell) at the midpoints of 6 mm length classes. Within the same length class, species followed by the same letter (a, b or c) do not differ (95% CIs do not overlap). Wild spectacled eiders in the study area ate almost no clams <12 mm long (see Fig. 1)

Species	Length (mm)	Dry mass (mg)		Ash mass (mg)		AFDM (mg)	
		Midpoint	95% CI	Midpoint	95% CI	Midpoint	95% CI
<i>N. radiata</i>	6.1–12.0	75a	74–76	59a	57–60	13a	12–14
	12.1–18.0	273a	269–278	216a	210–219	52a	50–55
	18.1–24.0	640a	629–651	504a	493–515	132a	125–139
	24.1–30.0	1209a	1189–1229	955a	933–976	263a	249–277
<i>M. calcaria</i>	6.1–12.0	37b	37–38	25b	24–25	12a	12–12
	12.1–18.0	175b	172–179	119b	117–122	56a	53–56
	18.1–24.0	449b	441–457	310b	304–316	136a	132–141
	24.1–30.0	1035b	1016–1054	725b	711–739	307b	298–317
<i>N. belloti</i>	6.1–12.0	98c	95–101	74c	72–77	22b	21–23
	12.1–18.0	459c	444–473	340c	329–351	120b	114–125

lower in *M. calcaria*. However, in the length range comprising 94% of the AFDM eaten by eiders (18 to 30 mm, Fig. 1), energy content was 19 to 43% higher in *M. calcaria* than in *N. radiata*. Even with its much greater ash content, *Nucula belloti* 12 to 18 mm long contained 80% more lipid, 2.6 to 2.9 times more nitrogen, and 2.2 to 3 times more energy than the other 2 species (Table 2).

The force needed to crush shells with a tensometer increased with shell length for *Macoma calcaria* and *Nucula belloti* (Fig. 3). *Nuculana radiata* showed a similar trend in shorter length classes; but at greater lengths, measurements for this species were quite variable because many shells were mildly to severely abraded around the umbo. *N. belloti* was far more difficult to crush than *M. calcaria* in the 12 to 18 mm length class, but did not differ from *N. radiata* of the same length (Table 2). For clams 12 to 24 mm long (78% of the eider diet, Fig. 1), *N. radiata* was much harder to crush than *M. calcaria*; however, for longer shells (19% of the diet), *N. radiata* was not consistently harder to crush because of frequent shell erosion.

Digestibility and gut retention time

For common eiders fed *Nuculana radiata* and *Macoma calcaria*, neither AE nor AE_N differed significantly between species, although the mean AE_N was 13% higher ($p = 0.177$) for *M. calcaria* (Table 3). Because of its higher shell content, *N. radiata* had greater values of cumulative excretion than *M.*

calcaria (Fig. 4A). However, the 2 species did not differ in excretion rate (Fig. 4B). Moreover, estimates of MRT in the gut did not differ within or between clam species for any collection duration (Table 4).

Functional responses

Of the AFDM eaten by wild spectacled eiders, 74% was from clams 18 to 24 mm long (Fig. 1). At 7 clam densities (50, 100, 200, 400, 800, 1200 and 1600 m^{-2}) and at the same depth in the sediments (4 cm), mean intake rates (no. s^{-1}) of freshly thawed *Macoma balthica* 18 to 24 mm long were the same for 4 white-winged scoters as for 1 spectacled eider (t -test comparing

Table 2. *Nuculana radiata*, *Macoma calcaria*, and *Nucula belloti*. Nitrogen, lipid, and energy content per clam (including shells), and force (mean \pm 1 SD, in Newtons) required to crush shells, in 6 mm length classes. Owing to small amounts of tissue in individual clams, values for nitrogen, lipid, and energy are for pooled samples of 5 clams (or 10 clams for 6 to 12 mm) in each length class. Within the same length class, species followed by the same letter (a or b) do not differ in crushing resistance (Bonferroni pair-wise comparisons, $p > 0.05$). Wild spectacled eiders in the study area ate almost no clams <12 mm long (see Fig. 1)

Species	Length (mm)	Nitrogen (mg)	Lipid (mg)	Energy (kJ)	Force (N)
<i>N. radiata</i>	6.1–12.0	0.71	2.14	0.21	20.85 \pm 5.12a
	12.1–18.0	3.09	7.64	0.95	37.37 \pm 10.28a
	18.1–24.0	8.37	16.37	2.20	34.33 \pm 12.8a
	24.1–30.0	17.80	29.00	4.09	24.80 \pm 8.95a
<i>M. calcaria</i>	6.1–12.0	0.71	2.16	0.21	No sample
	12.1–18.0	3.44	7.55	0.70	6.20 \pm 2.05b
	18.1–24.0	8.85	27.48	2.49	10.12 \pm 4.43b
	24.1–30.0	21.24	43.69	5.83	20.43 \pm 8.70a
<i>N. belloti</i>	6.1–12.0	1.54	2.39	0.42	25.79 \pm 13.10a
	12.1–18.0	9.04	13.59	2.13	39.65 \pm 20.04a

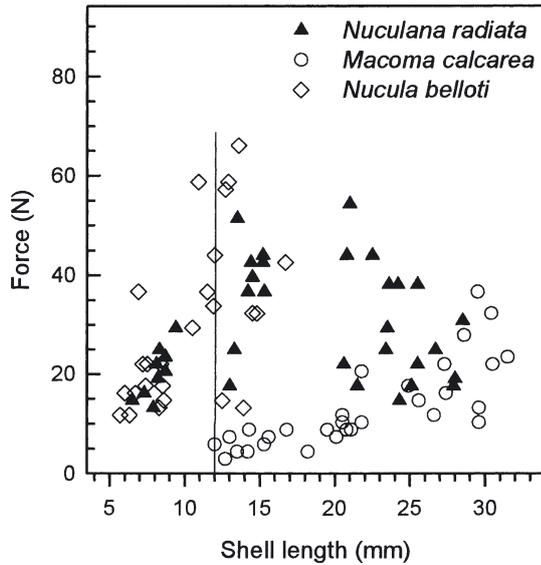


Fig. 3. Force in Newtons (N) required by a tensometer to crush shells of clams *Nuculana radiata*, *Macoma calcarea*, and *Nucula belloti* from the Bering Sea. Wild spectacled eiders in the study area ate almost no clams <12 mm long (see Fig. 1), as indicated by the vertical line

slopes of log-transformed functional responses, $p = 0.989$). For white-winged scoters, 4 birds feeding on *M. balthica* and 1 bird feeding on *Nuculana radiata* at the same 7 clam densities showed no difference in intake rate ($p = 0.388$). These results indicate that functional responses based on feeding trials with white-

Table 3. *Somateria mollissima*. Means (± 1 SD) of body mass before and after feeding experiments; of food (dry mass), ash, nitrogen, and energy ingested; of guano (dry mass), ash, nitrogen, and energy excreted; and of assimilation efficiency for energy (AE), nitrogen balance (NB), and AE corrected for nitrogen balance (AE_N) for common eiders fed 35 g fresh mass (including shells) of the clams *Nuculana radiata* and *Macoma calcarea*. p-values are for 2-tailed t-tests between species

		<i>N. radiata</i> (n = 4)	<i>M. calcarea</i> (n = 6)	p
Body mass	Initial mass (g)	2343 \pm 229	2239 \pm 214	0.484
	Final mass (g)	1867 \pm 119	1863 \pm 171	0.973
	Mass loss (%)	19.6 \pm 11.0	16.6 \pm 5.4	0.581
Ingesta	Food (g)	30.6 \pm 5.4	18.3 \pm 0.9	<0.001
	Ash (g)	24.3 \pm 4.3	12.6 \pm 0.6	<0.001
	Nitrogen (g)	0.43 \pm 0.08	0.40 \pm 0.02	0.309
	Energy (kJ)	105.6 \pm 18.5	103.6 \pm 5.0	0.802
Excreta	Guano (g)	20.1 \pm 1.8	16.5 \pm 1.3	0.007
	Ash (g)	3.8 \pm 0.2	1.8 \pm 0.5	<0.001
	Nitrogen (g)	0.69 \pm 0.18	1.00 \pm 0.41	0.194
	Energy (kJ)	44.0 \pm 9.9	47.1 \pm 9.6	0.637
Assimilation	AE (%)	57.3 \pm 12.7	54.4 \pm 10.0	0.700
	NB (kJ)	-9.4 \pm 8.5	-22.0 \pm 15.3	0.176
	AE_N (%)	67.3 \pm 6.9	75.9 \pm 10.1	0.177

winged scoters can be applied to spectacled eiders, and that trials using *M. balthica* can be applied to *N. radiata* as well as to its similar congener *M. calcarea*.

For scoters, intake rates increased with increasing clam density up to at least 1600 clams m^{-2} (Fig. 5). For *Macoma balthica* 18 to 24 mm long buried 4 cm deep in the sediments, the functional response was $I = 0.7483X / (591 + X)$, $r^2 = 0.91$, $p < 0.001$. At the same burial depth (4 cm), intake rate for larger *M. balthica* (24 to 30 mm) was $I = 0.4961X / (209 + X)$, $r^2 = 0.84$, $p < 0.001$. For smaller clams (18 to 24 mm), intake rates were much lower at greater burial depths (7 vs 4 cm): $I = 0.5396X / (682 + X)$, $r^2 = 0.83$, $p < 0.001$. The curve for smaller clams at 7 cm depth differed from the other 2 curves (F -test, $p < 0.04$). Because the curves showed reverse patterns at lower versus higher clam densities (Fig. 5), at 4 cm depth the curve for smaller versus larger clams did not differ statistically ($p = 0.64$). However, these 2 curves predict substantially different intake rates at higher clam densities, so the distinction between these curves was retained as biologically important.

In the present study, we did not measure intake rates of clams 24 to 30 mm long at a depth of 7 cm. However, if effects of clam length and depth in the sediments on intake rates are considered additive, then intake rates of clams 24 to 30 mm long at a depth of 7 cm can be estimated. This estimate was made by subtracting the decline in intake rate at 7 versus 4 cm for 18 to 24 mm clams from the intake rate for 24 to 30 mm clams measured at 4 cm depth, yielding the equation $I = 0.2955X / (139 + X)$. Regardless of depth in the sediments, fitted functional responses indicated that intake rates of smaller clams 18 to 24 mm long were limited by clam density up to at least 2000 m^{-2} , while intake rates of larger clams 24 to 30 mm long were more limited by handling time at densities $>400 m^{-2}$ (Fig. 5).

DISCUSSION

In the Bering Sea south of St. Lawrence Island, there appears to have been a long-term shift in dominant clam prey from *Macoma calcarea* to *Nuculana radiata* (Sirenko & Koltun 1992, National Research Council 1996). On their main wintering area 60 to 145 km south of the island, 12 spectacled eiders collected in March 2001 had eaten over 99% *N. radiata* and no *M. calcarea* (Lovvorn et al. 2003). A striking result of the latter study was that the eiders ignored a variety of prey

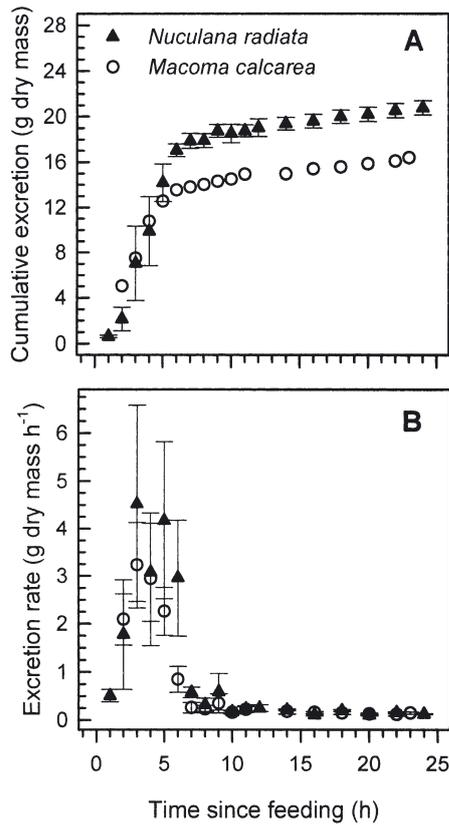


Fig. 4. *Somateria mollissima*. (A) Cumulative excretion and (B) excretion rate versus time since feeding for common eiders fed 35 g fresh mass (including shell) of clams *Nuculana radiata* (n = 4 birds) or *Macoma calcareia* (n = 6). Error bars are ±1 SE. Because of higher shell content, values of cumulative excretion were greater for *N. radiata* (paired *t*-test, *p* < 0.001); however, excretion rates did not differ between species (*p* > 0.25). Mean retention times from mouth to anus (MRT) also did not differ between species based on collection durations of 12, 18, and 24 h after feeding (see Table 4)

that are eaten elsewhere but were present there in low abundance, and focused their foraging on the most abundant prey. No diet data exist from before the

Table 4. Mean retention times from mouth to anus (MRT, ±1 SD) for common eiders fed 35 g fresh mass (including shells) of the clams *Nuculana radiata* (n = 4 eiders) and *Macoma calcareia* (n = 6 eiders), calculated for collection durations of 12, 18, and 24 h after feeding. MRT did not differ among collection durations (*p* = 0.168) or between clam species (*p* = 0.540), with no significant interactions (*p* = 0.825) (2-way ANOVA)

Species	Collection duration (h)		
	12	18	24
<i>Nuculana radiata</i>	4.68 ± 0.84	5.32 ± 0.82	5.95 ± 0.79
<i>Macoma calcareia</i>	4.58 ± 1.13	5.78 ± 2.39	7.04 ± 3.55

apparent shift in clam dominance. However, we presume the eiders ate mainly *M. calcareia* which was dominant then (Sirenko & Koltun 1992), and which they now often eat during spring migration in areas much closer to the island (Petersen et al. 1998) which have a sandier bottom and different benthic community. In shell lengths comprising 78% of AFDM eaten by eiders on their wintering area (12 to 24 mm, Fig. 1), shells of *M. calcareia* are much easier to crush in the gizzard; however, frequent shell abrasion in older *N. radiata* reduces this effect at shell lengths >30 mm (19% of the diet). Despite substantially higher ash content in *N. radiata*, the 2 clam species did not differ in gut retention time. However, differences in digestibility, in nitrogen, lipid, and energy content, and in burial depth in the sediments have important effects on the clams' relative foraging value.

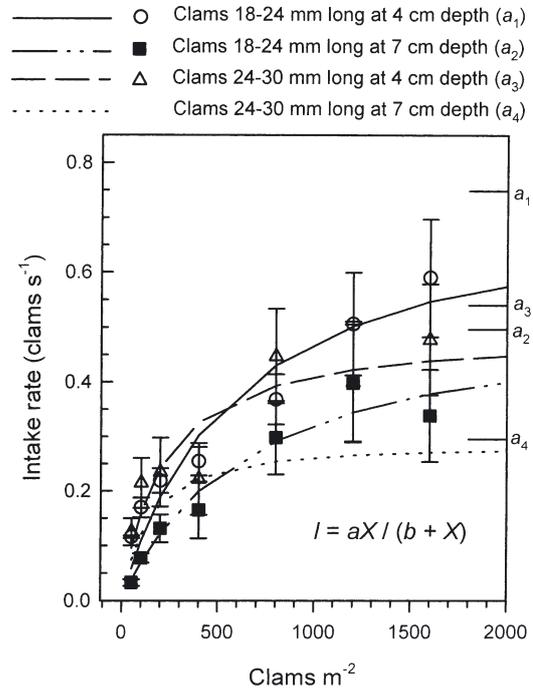


Fig. 5. *Melanitta fusca*. Functional responses of 4 white-winged scoters diving 1.8 m to feed on the clam *Macoma balthica* 18 to 24 and 24 to 30 mm long at depths in the sediments of 4 and 7 cm. The functional response for clams 24 to 30 mm long at 7 cm depth was estimated by subtracting the decline in intake rate at 7 versus 4 cm for clams 18 to 24 mm long from the equation for clams 24 to 30 mm long at 4 cm depth. The model is $I = aX / (b + X)$, where *I* is the number of prey items ingested per second at the bottom, *a* is the handling time coefficient or the asymptote for the maximum rate at which scoters can handle prey regardless of prey density, *X* is the number of prey m⁻², and *b* is the search time coefficient or the prey density at an intake rate of 0.5*a*. Values of parameter *a* numbered for respective curves are indicated. For fitted equations and statistical tests among curves, see text. Error bars are ±1 SE

Composition and crushing resistance of clams

In length classes comprising 94 % of the eiders' diet (18 to 30 mm, Fig. 1), energy content (including shell) was 13 to 43 % higher in *Macoma calcaria* than in *Nuculana radiata* (Table 2). This difference resulted partly from the 51 to 68 % higher lipid content of *M. calcaria*. Lipid content of bivalves often varies seasonally, increasing during periods of abundant food and decreasing during relative food scarcity (Wenne 1985, Polak et al. 1987). Peak body reserves of lipid and glycogen often culminate in gamete production, leaving body reserves depleted (Ansell 1974, Davis & Wilson 1983). The annual cycle of body reserves and reproduction has not been documented in *M. calcaria* or *N. radiata* in our study area. However, based on studies of *M. calcaria* and other species in Denmark and Greenland, we would expect peak reserves after the spring bloom associated with ice melt in May, spawning from late June to early August, and an annual minimum of reserves in March and April (Thorson 1936, Muus 1973, Petersen 1978). *N. radiata* is a labial palp deposit-feeder that probably broods its young internally (see *Nuculena (Leda) pernula*, Ockelmann 1958). Thus, it may differ in annual reserve strategy from *M. calcaria*, which is a siphonate deposit- and filter-feeder with pelagic larvae (Muus 1973, Kranz 1974). Such differences might explain the higher lipid and energy content of *M. calcaria* than in *N. radiata* during March and April in our study area. In August in Frobisher Bay of the eastern Canadian Arctic (Wacasey & Atkinson 1987), the energy content without shells of *M. calcaria* (17.97 kJ [g dry mass]⁻¹) was also higher than in *N. minuta* (16.37 kJ [g dry mass]⁻¹) or *N. pernula* (16.83 kJ [g dry mass]⁻¹), and lower than in *Nucula belloti* (19.95 kJ [g dry mass]⁻¹), as in our study.

Crushing resistance varied substantially among clam species. The very high crushing resistance of *Nucula belloti* 10–14 mm long (Fig. 3) may partly explain why it was eaten in only trace amounts by the eiders, although it had far greater abundance and biomass than the other 2 clam species in that length range (Lovvorn et al. 2003). In the length range encompassing 78 % of AFDM eaten by eiders on their wintering area (12 to 24 mm), *Nuculana radiata* was far harder to crush than *Macoma balthica*. However, abrasion of shells near the umbo of older *N. radiata*, at times so severe that the shell was transparent, eliminated this difference at lengths >26 mm (Fig. 3). The cause of this damage is unknown. Unlike most *M. calcaria*, *N. radiata* of all sizes live near the sediment surface where they are more subject to abrasion by moving sediments (Stanley 1970). Predators such as crabs may also play a role in shell abrasion (Feder & Jewett 1981). *Chionoecetes* spp. crabs were very abundant in 1999 and 2001,

and at least some crab species attack mainly the umbo area (Elnor 1978) where most damage to *N. radiata* occurred. Such attacks may increase with climate trends that enhance the local density of predators such as *Chionoecetes* spp. (Zheng & Kruse 2000, Rosenkranz et al. 2001). Regardless of cause, this shell damage reduces the disadvantage to eiders of the otherwise higher crushing resistance of *N. radiata*. Moreover, heat generated by grinding shells in the gizzard might substitute for thermogenesis in eiders, mitigating the higher costs of crushing undamaged *N. radiata* (de Leeuw et al. 1998). The latter effect will be difficult to discriminate experimentally from other aspects of the heat increment of feeding (Kaselloo 2002, Kaselloo & Lovvorn 2003).

Digestibility and gut retention time

The higher ash content (thicker shell) of *Nuculana radiata* might be expected to decrease its digestibility or passage rate relative to *Macoma calcaria*. Higher bulk of calcium carbonate shell might limit nutrient assimilation by mechanically restricting access of digestive enzymes to the ash-free component, by raising the pH in the gut above the optimal range for enzyme function, or by reducing diffusion of nutrients from the lumen to the gut wall (see Speakman 1987). However, *MRT* did not differ between clam species for the meal size (35 g) in this study. Although the 13 % greater digestibility of *M. calcaria* ($AE_N = 76$ vs 67 %) was not significant at the 0.05 level ($p = 0.177$), this difference had important effects on calculations of total energy assimilated (gross energy vs assimilated energy, see below).

For free-ranging common eiders, Guillemette (1994) estimated that a full gizzard contains about 20 g of mussels and that the size of a full meal (maximum typically eaten in a single foraging bout) ranges from 60 to 100 g. Although 35 g is within the range of potential meals in free-ranging eiders, it is possible that the bulk of ash in larger meals might have greater effects on assimilation efficiency and retention time. In experiments, however, such amounts would have to be forced to the birds incrementally, allowing them to clear their gizzards after each feeding. Resulting levels of stress to the birds might therefore confound digestive measurements.

Effects of abundance, length, and burial depth on clam intake rates

For smaller clams (18 to 24 mm long) that comprised 74 % of the AFDM consumed by wild spectacled eiders

(Fig. 1), projected intake rates increased with increasing clam density up to at least 2000 m^{-2} regardless of depth in the sediments (Fig. 5). For larger clams (24 to 30 mm long) that made up 19% of the diet, intake rate increased more slowly at higher clam densities, being more limited by handling time at densities $>400 \text{ m}^{-2}$. For clams of the same length (measured only for clams 18 to 24 mm long), intake rates were substantially lower at the deeper burial depth. Thus, the effects of long-term changes in clam abundance on intake rates (no. s^{-1}) depend strongly on clam size and depth in the sediments.

For clams buried 4 cm deep at a density of 1200 m^{-2} , increased shell length from 18 to 24 mm to 24 to 30 mm reduced intake rates of scoters by 16% (Fig. 5). With its short siphon, *Nuculana radiata* of all length classes is positioned within this top depth layer (based on boxed cores, J. M. Grebmeier, pers. obs.). Consequently, this shell length effect may explain why free-ranging spectacled eiders consumed this species in greater proportion than available in the 18 to 24 mm length class, and in lower proportion than available in the 24 to 30 mm length class (Fig. 1).

Effects of shell length on intake rates of *Macoma calcaria* are complicated by increasing burial depth with increasing clam size. The depth distribution of shell lengths of *M. calcaria* has not been reported. However, at 5 subtidal sites with silt-clay sediments in San Francisco Bay, California (1 mm sieve), lengths of *M. balthica* ranged from 8 to 16 mm (mean 13.1) at 0 to 5 cm depth, 13 to 20 mm (mean 18.3) at 5 to 10 cm depth, and 20 to 30 mm (mean 24.3) at 10 to 20 cm depth (V. K. Poulton & J. R. Lovvorn unpubl. data). Based on these data, we expect that most *M. calcaria* >18 mm long are at depths of 7 cm or more. In silt-clay sediments, Lovvorn (1989) found that canvasbacks *Aythya valisineria*, large diving ducks which commonly feed on *M. balthica* during winter, generally did not excavate plant tubers in the field at depths >10 cm. Thus, our functional response data for 7 cm depth are applicable to *M. calcaria* 18 to 24 mm long, and the estimated curve for clams 24 to 30 mm long at 7 cm depth can be applied to *M. calcaria* of that length.

Species differences in nitrogen and energy intake and assimilation

How do abundance, digestibility, and length-dependent nutrient content and burial depth of the 2 clam species interact to affect nitrogen and energy acquisition by the eiders? Based on curves in Fig. 5 and values in Table 2, functional responses were converted from number of prey consumed per second to inges-

tion rates of nitrogen (mg s^{-1}) and gross energy (GE , kJ s^{-1}) for *Nuculana radiata* and *Macoma calcaria* at their respective burial depths (Fig. 6, Table 5). Digestibility of protein in flesh has been estimated at about 83% (Zwarts & Blomert 1990); however, digestibility of nitrogen was not measured in our study, and was not accounted for in these calculations. Functional responses were also modeled in terms of rates of energy assimilated (Fig. 7), calculated as GE intake (kJ s^{-1} , Fig. 6B) \times assimilation efficiency of energy (AE_N , using different values for the 2 species in Table 3).

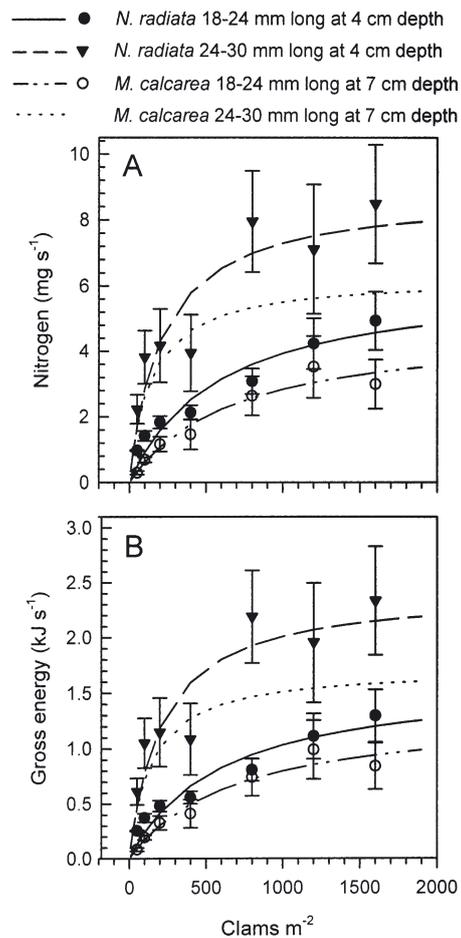


Fig. 6. *Melanitta fusca*. Functional responses of 4 white-winged scoters feeding on the clams *Nuculana radiata* and *Macoma calcaria* in terms of (A) nitrogen (mg s^{-1}) and (B) gross energy (kJ s^{-1}), calculated from curves in Fig. 5 and values in Table 2. For fitted parameters see Table 5. Curve for *M. calcaria* 24 to 30 mm long at 7 cm depth is based on a functional response with an estimated depth effect (Fig. 5). Curves for smaller clams (18 to 24 mm) differ between depths (F -tests, $p = 0.012$ for nitrogen, $p = 0.059$ for gross energy), and curves for smaller clams at each depth differ from that for larger clams (24 to 30 mm) at 4 cm depth ($p < 0.001$ for both nitrogen and gross energy)

Table 5. Fitted parameters of the functional responses in Figs. 6 & 7 for white-winged scoters feeding on the clams *Nuculana radiata* and *Macoma calcaria* of different length classes (18 to 24 mm, 24 to 30 mm) buried in sand-filled trays at depths of 4 and 7 cm. See Fig. 5. for definitions of model parameters. Parameters for clams 24 to 30 mm long at 7 cm depth are based on a functional response with an estimated depth effect (Fig. 5). Values of b and r^2 are the same for both species for all 3 dependent variables, because the same functional response equations were used. All models were significant at $p < 0.001$

Parameter	Parameter	<i>Nuculana radiata</i>				<i>Macoma calcaria</i>			
		18 to 24 mm		24 to 30 mm		18 to 24 mm		24 to 30 mm	
		4 cm	7 cm	4 cm	7 cm	4 cm	7 cm	4 cm	7 cm
Nitrogen (mg s^{-1})	a	6.26	4.52	8.83	5.14	6.62	4.78	10.54	6.28
Gross energy (kJ s^{-1})	a	1.65	1.19	2.43	1.45	1.86	1.34	2.89	1.72
Assimilated energy (kJ s^{-1})	a	1.11	0.80	1.64	0.97	1.41	1.02	2.19	1.31
	b	591	682	209	139	591	682	209	139
	r^2	0.91	0.83	0.84	1.00	0.91	0.83	0.84	1.00

Larger *Nuculana radiata* (24 to 30 mm long) were the most valuable food at all clam densities (Figs. 6 & 7). At a density of 1200 m^{-2} (within the range observed in the field), larger *N. radiata* (≤ 4 cm deep) yielded 34% higher intake of nitrogen and gross energy, and 19% higher assimilated energy, than *Macoma calcaria* of the same length (mostly ≥ 7 cm deep). At 1200 clams m^{-2} , smaller *N. radiata* 18 to 24 mm long (≤ 4 cm deep) yielded 38% higher nitrogen intake, 29% higher gross energy, and 14% higher assimilated energy than *M. calcaria* of the same length (≥ 7 cm deep). These results indicate that, owing to its shallower burial

depth, *N. radiata* always has higher foraging value than *M. calcaria* of the same length, despite the higher digestibility and higher nitrogen and energy content of *M. calcaria*. This superior value of *N. radiata* within the same size class increases with increasing shell length. (Note that differences in crushing resistance are not considered here.) Conversely, at 1200 clams m^{-2} , larger *M. calcaria* (24 to 30 mm long, ≥ 7 cm deep) yielded 34% higher nitrogen intake, 39% higher gross energy, and 58% higher assimilated energy than smaller *N. radiata* (18 to 24 mm long, ≤ 4 cm deep). As emphasized by the latter comparisons, relative foraging value depends strongly on the size (age) structures of the different clam populations, which vary with annual and seasonal differences between species in recruitment, growth, and mortality.

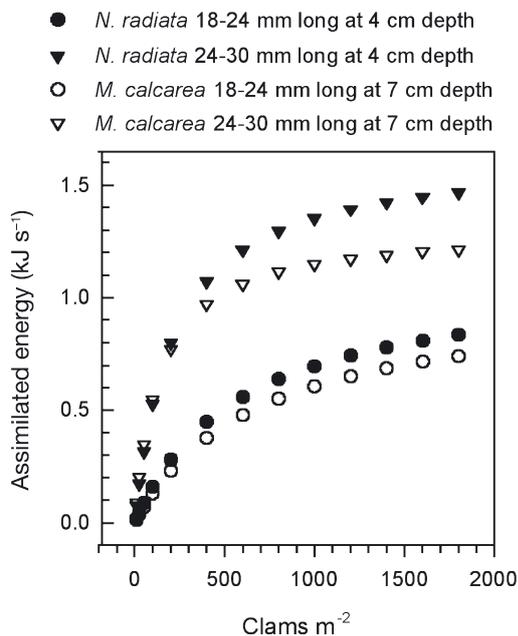


Fig. 7. Modeled functional responses of white-winged scoters feeding on clams *Nuculana radiata* and *Macoma calcaria* in terms of the rate of energy assimilated (kJ s^{-1}), calculated as gross energy intake rate (kJ s^{-1} , Fig. 6B) \times assimilation efficiency of energy (AE_N , Table 3). For fitted parameters see Table 5

Impacts of the clam species shift on eider foraging

The present study has examined a comprehensive array of factors affecting the relative foraging value of bivalve prey. We conclude that impacts of long-term benthic change on spectacled eiders depend not only on shifts in total clam abundance, but also on species differences in digestibility, size structure, and size-dependent nutrient content and burial depth. The generally higher nitrogen, lipid, and energy content of *Macoma calcaria*, an advantage which increases with increasing shell length, is offset by its greater burial depth which also increases with shell length. The influence of size-dependent effects will depend on seasonal and annual variations in recruitment, growth, and mortality among species. Investigating the net results of these interacting factors will require computer simulations of intake rates for different clam abundances, species composition, and size frequencies observed during long-term studies that span the eider decline (Sirenko & Koltun 1992, Grebmeier & Cooper 1995, Grebmeier & Dunton 2000). Energy assimilated

must then be compared with estimated energy costs of foraging and other activities, to infer whether the eiders' energy balance has been adversely affected (Lovvorn & Gillingham 1996).

Climate shifts may also have affected other clam predators in the Bering Sea, including walruses, seals, fish, crabs, and snails (Wyllie-Echeverria & Wooster 1998, Zheng & Kruse 2000, Connors et al. 2002). For these other benthic feeders, an approach such as ours might be useful in evaluating effects of long-term changes in numbers, species, and size structure of prey (Edwards & Huebner 1977, Franz 1977, Hanson et al. 1989, Eggleston et al. 1992, Nakaoka 1996).

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