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RELATIVE FORAGING VALUE TO LESSER SCAUP DUCKS OF NATIVE AND EXOTIC CLAMS FROM SAN FRANCISCO BAY

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Abstract. Invasions of exotic invertebrates have greatly altered many aquatic communities, but impacts on the foraging energetics of predators seldom have been assessed. In San Francisco Bay, California (USA), a major community change occurred with introduction of the Asian clam (*Potamocorbula amurensis*) in 1986. This species now greatly outnumbers the previous clam prey of a variety of sharks, rays, sturgeon, flatfish, and crabs, as well as several diving duck species for which the bay is the most important wintering area on the U.S. Pacific Coast. *P. amurensis* also accumulates much higher levels of some contaminants than the formerly dominant prey. Because alteration of the food base or contaminated foods on wintering areas may be factors in the population decline of scaup ducks, effects of this exotic invasion are important to assess. For Lesser Scaup (*Aythya affinis*), we studied effects of differences in nutrient content, digestibility, crushing resistance of shells, areal density, size, and depth in the sediments on the relative foraging value of exotic *P. amurensis* vs. the formerly dominant native clam *Macoma balthica*. *P. amurensis*, including shells, had higher nitrogen and energy content per clam of the same length class, and higher digestibility of energy, than *M. balthica*. Gut retention time did not differ between clam species, so their relative profitability for scaup was determined mainly by the intake rate of digestible nutrients during short, costly dives. For scaup foraging in an aquarium 1.8 m deep, intake rates (number of prey per second) of food items buried in sand-filled trays increased with increasing prey density up to at least 4000 prey/m^2. For items buried 3 cm deep, intake rates did not differ for prey <6 mm long vs. prey 6–12 mm long; however, intake rates were much lower when prey were deeper in the sediments (6 cm vs. 3 cm). In the field, a much higher percentage of *P. amurensis* were in the length range most commonly eaten by Lesser Scaup (<12 mm), and unlike *M. balthica*, almost all *P. amurensis* were in the top 5 cm of sediments where scaup intake rates are highest. In tensometer measurements, shells of *P. amurensis* were much harder to crush than shells of *M. balthica*, which might partly offset the apparent energetic advantages of *P. amurensis*. In many respects, the exotic *P. amurensis* appears to be a more valuable food than the native *M. balthica* for Lesser Scaup. However, because *P. amurensis* accumulates much higher levels of some contaminants, this exotic invasion increases the risk of toxicity to scaup and a range of other benthic predators.

Key words: Aythya affinis; digestibility; diving ducks; exotic invasions; functional response; gut retention time; intake rates; Lesser Scaup; Macoma balthica; Potamocorbula amurensis; *San Francisco Bay; scaup feeding behavior.*

INTRODUCTION

Invasions of exotic plants and animals have had major impacts on many aquatic communities worldwide (Posey 1988, Ludyanskiy et al. 1993, Stewart and Haynes 1994, Cohen and Carlton 1998, Kolar and Lodge 2000). In some cases, vertebrate consumers have used and even focused on introduced organisms (Perry and Uhler 1981, French 1993, Baldwin and Lovvorn 1994, Hamilton et al. 1994, Custer and Custer 1996). However, the foraging value of exotic vs. native species is seldom known (French and Bur 1996). In San Francisco Bay, California, USA, benthic predators experienced a major change in prey communities with the

invasion of the Asian clam (*Potamocorbula amurensis*) in 1986. This species spread rapidly throughout the bay, mostly displacing the former community (Carlton et al. 1990, Nichols et al. 1990). The bay is important habitat for a variety of predators of bivalves, including diving ducks, sharks, rays, sturgeon, flatfish, and crabs (Ganssle 1966, McKechnie and Fenner 1971, Russo 1975, Nichols and Pamatmat 1988, Urquhart and Regalado 1991). Until this study, however, *P. amurensis* had not been compared to formerly dominant prey in terms of foraging value (intake and assimilation of food at a given abundance).

The issue of comparative foraging value is especially relevant to several species of diving ducks for which San Francisco Bay is the most important wintering area on the U.S. Pacific Coast (Bellrose 1980). For example, in the winters of 1989 and 1990, Lesser and Greater Scaup (*Aythya affinis, A. marila*) accounted for 43–

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47% of waterfowl in the bay. In midwinter 1989, 131 400 scaup were found in the bay; this number was 92% of all scaup counted in the Pacific Flyway (Accurso 1992). It has been suggested that a 20-year decline in breeding populations of scaup, especially of Lesser Scaup, is related to a deteriorating food base or contaminated foods on migration and wintering areas (Austin et al. 2000). Lesser Scaup were recently found to feed almost entirely on *P. amurensis* in a large area of northern San Francisco Bay (San Pablo Bay; J. Y. Takekawa, S. E. Wainwright-De La Cruz, and A. K. Miles, *unpublished data*). Benthic densities and species composition in the bay can fluctuate dramatically with annual and long-term variations in freshwater inflow (Nichols and Thompson 1985, Nichols et al. 1990, Poulton et al. 2004). Thus, information on the profitability (gain minus cost) of foraging on *P. amurensis* and other common species is important to understanding and predicting the bay's carrying capacity for predators of bivalves.

A further concern is that *P. amurensis* accumulates much higher levels of selenium than do other bivalves in the area (Linville et al. 2002). Diving ducks and sturgeon that feed on bivalves have shown elevated selenium levels in the past that may have increased since *P. amurensis* invaded (Ohlendorf et al. 1986, Urquhart and Regalado 1991, Hothem et al. 1998, Linville et al. 2002). However, uptake of contaminants by mobile predators often shows weak and variable correlations with concentrations in food because of variable amounts eaten in different areas (Skorupa and Ohlendorf 1991, Lovvorn and Gillingham 1996a). Larger (older) clams also can have higher levels of some contaminants that accumulate over time (Strong and Luoma 1981, Goede et al. 1993). A better understanding of factors affecting intake rates of different species and sizes of clams at different sites would help to identify situations in which contaminant exposure of predators is greatest.

The rate of acquisition of energy and nutrients 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). Change in intake rate with prey density, known as the functional response, is a basic component of a number of models of waterbird foraging (Myers et al. 1980, Wanink and 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 (Takekawa 1987, Giles 1990, Lovvorn and Gillingham 1996b, Richman and Lovvorn 2003). Prey depth in the sediments has important effects on the functional responses of crabs and shorebirds eating clams (Wanink and Zwarts 1985, Lipcius and Hines 1986, Zwarts and Blomert 1992, Seitz et al. 2001), but effects of prey depth seldom have been studied for diving ducks (Carbone 1995). Nutrient and energy content, digestibility, and crushing resistance of shells can vary with both species and size of bivalves (Beukema and de Bruin 1977, Jorde and Owen 1988, Bustnes and Erikstad 1990, Piersma et al. 1993), and a number of studies have shown size selection of bivalves by diving ducks (Draulans 1982, 1984, Bustnes and Erikstad 1990, de Leeuw and van Eerden 1992, Bustnes 1998, Hamilton et al. 1999). In these studies, 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. Resistance of shells to crushing in the gizzard may also affect selection of species and sizes of bivalve prey (Navarro et al. 1989).

Moreover, because the volume of air in the respiratory system and plumage is compressed with increasing depth under water, work against buoyancy during descent and bottom foraging also changes with water depth (Lovvorn and Jones 1991, Lovvorn et al. 1991, Lovvorn 1994). Consequently, variations in dive depth may affect the profitability and resulting selection of prey of different densities, sizes, and depths in the sediments (Beauchamp et al. 1992, de Leeuw and van Eerden 1992). Thus, to be relevant to field situations, foraging experiments with diving ducks are best done at typical dive depths.

For the exotic *P. amurensis* and the formerly dominant native clam *Macoma balthica*, we measured the energy and macronutrient content, crushing resistance of shells, digestibility, and gut retention time by captive Lesser Scaup. We also determined the functional responses of scaup foraging on food items of different sizes buried at different depths in sand-filled trays at the bottom of an aquarium 1.8 m deep. Given the high densities sometimes achieved by *P. amurensis* in the field (Carlton et al. 1990), we did repeated foraging trials at densities up to 7000 prey/m². For such extensive experiments, field efforts indicated that collecting enough small clams (over 30 000 clams <12 mm long) from San Francisco Bay was financially impractical. In later years, we hired a waterman in Chesapeake Bay to collect *M. balthica* with a commercial clam dredge, but the animals that he collected were mostly too large for relevant experiments with scaup. Moreover, the specially designed dive tank that we used (see *Methods*) was in Manitoba; transporting and maintaining such large numbers of live brackish-water clams for several months of experiments in this freshwater tank were infeasible, and importing live exotic clams into Canada was not allowed.

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 and McGrorty 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 and Quammen 1982, Peterson and Skilleter 1994, Ansell 1995, Tallqvist 2001), and measured burrowing rates of 0.07–0.13 mm/s 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 and Peterson 1994), retracting siphons would not prevent ingestion by ducks. Thus, predation rates on nonliving prey should be reasonably similar to those on live clams. Consequently, to assess effects of food-item size and depth in the sediments on intake rates, we used tubers of the submersed plant *Potamogeton pectinatus* as a surrogate food after validating that intake rates of tubers and freshly thawed clams of similar size did not differ.

By combining data on functional responses and clam composition and digestibility, we then estimated the relative foraging value of *P. amurensis* and *M. balthica* for Lesser Scaup. This comparison is the first quantitative assessment of the impacts of *P. amurensis* invasion on the foraging energetics of a major clam predator in San Francisco Bay.

METHODS

Composition and crushing resistance of clams

For nutrient analyses, *P. amurensis* and *M. balthica* were collected at five sites in San Pablo Bay, in northern San Francisco Bay, in October–December 1999 (see Poulton et al. [2002] for map of collection sites). Shell lengths were measured along the anterior–posterior axis to the nearest 0.1 mm, and were divided into 6 mm length classes (≤6.0 mm, 6.1–12.0 mm, 12.1–18.0 mm, 18.1–24.0 mm, and 24.1–30.0 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 was not included in calculating AFDM.

Energy analyses with bomb calorimetry required larger samples (~0.5 g dry mass including shell) than were contained in most individual clams (see *Results*). Thus, we pooled five whole clams for each species and length class, except for *P. amurensis* 6–12 mm long, for which 10 clams were pooled. Nitrogen and lipid analyses were done on meat removed from shells. Lipid content, determined by extraction with petroleum ether, required far more material than was contained in single clams, so multiple clams were again pooled for each species and length class. Subsamples of the dried-flesh homogenate were analyzed for nitrogen content with an elemental analyzer (Fison Instruments, Milan, Italy).

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.

Scaup consume whole clams and crush the shells in their gizzard. Consequently, we used a tensometer (double proving ring, Model EI78-0900, Soiltest, Evanston, Illinois, USA) 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 of clams

Feeding trials were conducted November–December 1999 at the Delta Waterfowl and Wetlands Research Station in Manitoba, Canada. Lesser Scaup used in experiments were randomly chosen from a captive flock raised from eggs collected in Ceylon, Saskatchewan, and Jesse Lake, Alberta in July 1999. When not involved in feeding trials, the scaup were housed in an indoor aviary and were fed a diet of two parts turkey starter pellets (25% crude protein, 2.5% crude fat, 6% crude fiber) to one part wheat. Grit was not supplied for two weeks before and during the trials.

For digestibility trials, *P. amurensis* and *M. balthica* collected in San Pablo Bay (see previous section) were frozen and shipped overnight to Manitoba. Shell lengths of clams fed to the birds corresponded to lengths eaten by scaup in San Francisco Bay (<12 mm; J. Y. Takekawa, S. E. Wainwright-De La Cruz, and A. K. Miles, *unpublished data*).

Eight Lesser Scaup, four of each sex, 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 (~25 g fresh mass including shells), and (4) a 48-h excreta collection period. Each bird was habituated to the 4-d experiment, including force-feeding of clams and excreta collection procedures, two weeks before the actual experiment. The amount of clams fed to the birds (25 g) was the maximum that they would consistently retain during force-feeding.

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 (Saint-Gobain Performance Plastics, Akron, Ohio, USA) 25 cm long and 2 cm in diameter was slid down the throat, pulled back to the top of the proventriculus, and flushed with distilled water from a squeeze bottle. This method of intubation is commonly used in digestibility studies with chickens (Sibbald 1979), ducks

PLATE 1. Female Lesser Scaup feeding on prey items in a sand-filled tray at the bottom of a dive tank. Photo credit: F. Greenslade.

(Jorde and Owen 1988), and seabirds (Kirkwood and Robertson 1997). Scaup 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 birds were fed 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°–15°C with natural photoperiod (10 L:14 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 were frozen until analyzed. Excreta were later freeze-dried to constant mass, and subsamples were ground and homogenized. Content of energy, lipid, nitrogen, and ash were measured as previously described.

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 following formula:

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

where GE_{in} and GE_{out} are gross energy ingested and excreted (in kilojoules). Assimilated energy was corrected for nitrogen balance (NB) by the following formula:

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

where

$$NB = (N_{in} - N_{out}) \times 36.5 \text{ kJ/g N.} \qquad (3)$$

In Eq. 3, N_{in} and N_{out} are nitrogen ingested and excreted, and 36.5 kJ/g N is the mean energy content per gram of urine-nitrogen in birds (Titus et al. 1959, Sibbald 1982). Correction for nitrogen balance is needed because the energy in excreta from endogenous sources (e.g., protein breakdown products, gut epithelial cells, enzymes) can otherwise cause underestimates of assimilation efficiency.

Gut retention times

The time required to process food in the gut can be longer than the time 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 retention time in the gut can affect acquisition of nutrients and energy (Guillemette 1994, 1998). Mean retention time in the gut from mouth to anus was calculated as

$$MRT = \sum_{i=1}^{n} E_i t_i \bigg/ \sum_{i=1}^{n} E_i \qquad (4)$$

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 depend on how long sampling is continued beyond the time when most excretion of a meal has occurred (Hilton et al. 1998). To ensure that this variation did not affect tests between *P. amurensis* and *M. balthica*, 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 in a large concrete tank ($2 \times 5 \times 2$ m deep) with a water depth of 1.8 m. Plate glass windows in walls of the tank allowed observations and video filming of the ducks underwater. Lesser Scaup were trained to dive and feed in a sand-filled tray (0.5 m wide $\times$ 1 m long $\times$ 9 cm deep) at the bottom of the tank for at least two weeks before experiments (see Plate 1).

Four birds (two of each sex) foraged for two length classes of prey (≤6.0 mm and 6.1–12.0 mm) at 10 densities from 50 to 4000 prey/m², at two depths in the sand (3 cm and 6 cm); and on prey <6 mm long at 7000/m² at the 6 cm depth. We purchased belowground

TABLE 1. Data (mean ± 1 SD) for the clams *Potamocorbula amurensis* and *Macoma balthica* in 6-mm length classes: dry mass, composition of dry mass per clam including shell, and force (in Newtons) required to crush shells in a tensometer.

Length (mm)	Dry mass (mg)	Ash (mg)	AFDM (mg)	Nitrogen (mg)	Lipid (mg)	Energy (kJ)	Force (N)
P. amurensis							
6.1–12.0	70.6[a] ± 35.6	57.4[a] ± 28.0	9.1[a] ± 5.2	0.39	0.20	0.15	10.80 ± 6.61
12.1–18.0	263.5[b] ± 112.4	255.0[b] ± 125.2	29.0[b] ± 9.3	1.48	0.95	0.48	60.94 ± 33.28
18.1–24.0	571.6[c] ± 87.1	522.1[c] ± 90.7	49.9[c] ± 6.4	2.88	1.63	0.76	84.44 ± 7.72
M. balthica							
6.1–12.0	31.6[a] ± 7.1	22.7[a] ± 7.2	9.7[a] ± 2.7	0.22	0.26	0.05	1.15* ± 0.45
12.1–18.0	151.8[b*] ± 38.6	121.7[b*] ± 30.9	28.4[b] ± 8.8	1.40	0.67	0.27	12.97* ± 8.88
18.1–24.0	273.2[c*] ± 84.5	236.3[c*] ± 65.9	38.6[c] ± 16.9	2.33	1.04	0.38	10.28* ± 6.33

Notes: AFDM, ash-free dry mass. Nitrogen, lipid, and energy contents are for pooled samples necessitated by small amounts of tissue in individual clams; thus, no SD or statistical results are given. For other variables, values followed by the same letter do not differ within species; significant differences between species are indicated by asterisks (Bonferroni pairwise comparisons, $\alpha = 0.05$).

tubers of the submersed plant *Potomogeton pectinatus* (Wildlife Nurseries, Oshkosh, Wisconsin, USA) and cut them to appropriate length for foraging experiments. Experiments with tubers allowed us to assess the importance of characteristic differences in burial depth of *P. amurensis*, which has a very short siphon and is always near the sediment surface vs. *M. balthica*, which has a long siphon and increases its burial depth with clam size (Poulton et al. 2002, 2004). To verify that intake rates of tubers were the same as for freshly thawed clams of the same length, we did comparative trials with two of the experimental birds (one male, one female) eating the clam *Nuculana radiata*, which is similar to *P. amurensis* in size, shape, and shell thickness. Compared to *P. amurensis* of the same length class (<12 mm), *N. radiata* contained on average 59 vs. 57 mg of ash (shell content), and 13 vs. 9 mg AFDM. For all experiments, prey densities were presented in random order to randomly selected birds.

Prey items were counted and uniformly distributed on the bottom of the tray. Prey items were then covered with clean sand to a depth of 3 or 6 cm, depending on the trial. Sand depth (and thus burial depth of prey) was established with wooden scrapers constructed to create depths of 3 or 6 cm above the bottom of the tray. Excess sand was scraped to the side and removed. The tray was lowered to the bottom and raised after the trial with a winch that slid on a track above the tank. After the foraging bout, remaining prey items were counted after washing the sand through a 2-mm mesh screen. The number of prey consumed was calculated by subtraction. Time spent foraging at the bottom (probing the sand) was measured from video films as the time the bill entered the sand until the time the bill exited 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 scaup feeding on *P. pectinatus* tubers and *N. radiata* clams were fitted with Michaelis-Men-

ten equations (Marquardt method, PROC NLIN; SAS Institute 1987). In the equation $I = aX/(b + X)$, I is the number of prey consumed per second at the bottom, X is the number of prey per square meter, a is the handling time coefficient or the maximum rate at which prey items can be consumed regardless of prey density, and b is the search time coefficient or the prey density at an intake rate of $0.5a$ (Lovvorn and Gillingham 1996*b*). Functional responses for different combinations of prey size and depth were examined for differences with F tests (Chatterjee et al. 2000).

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 (including a series of dives) alternate cyclically with preening and resting periods throughout a 24-h period (Poulton et al. 2002). Because of the high energy cost of diving (Stephenson 1994, Kaseloo 2002), intake rate should be maximized during each dive to minimize time underwater, with dive bouts simply being terminated upon satiation (Lovvorn and Gillingham 1996*b*). 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).

RESULTS

Composition, crushing resistance, and digestibility of clams

Potamocorbula amurensis including shells had about twice the dry mass and 2–3 times the ash content of *Macoma balthica* of the same length classes, but the meat content (ash-free dry mass) was similar between species (Table 1). Regressions of fresh mass including shell (M_F), dry mass including shell (M_D), and AFDM on shell length (L) were $M_F = 0.0638 \ L^{3.179}$, $M_D = 0.0540 \ L^{3.136}$, and AFDM $= 0.0242 \ L^{2.585}$ for *P. amurensis*; and $M_F = 0.0357 \ L^{3.141}$, $M_D = 0.0271 \ L^{3.080}$, and AFDM $= 0.0590 \ L^{2.228}$ for *M. balthica* ($r^2 = 0.97$–0.98,
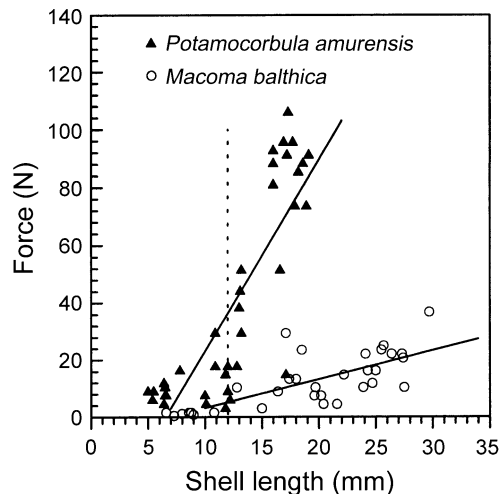
FIG. 1. Force in Newtons (N) required by a tensometer to crush shells of the clams *Potamocorbula amurensis* and *Macoma balthica*. Regressions of crushing force F_c vs. shell length L were $F_c = -43.55 + 6.66L$ ($r^2 = 0.69$, $P < 0.001$) for *P. amurensis*, and $F_c = -6.94 + 1.01L$ ($r^2 = 0.54$, $P < 0.001$) for *M. balthica*. Free-ranging Lesser Scaup in San Francisco Bay ate mainly clams <12 mm long (delineated by the vertical dotted line). In that length range, the crushing resistance (mean $\pm$ 1 SD) for *P. amurensis* (10.80 $\pm$ 6.61 N, $n = 15$ clams) was more than nine times greater than for *M. balthica* (1.15 $\pm$ 0.45 N, $n = 7$ clams) in a Bonferroni pairwise comparison ($P < 0.001$; Table 1).

all $P < 0.001$). Nitrogen content per clam was somewhat higher in *P. amurensis* in all length classes, as was lipid content except in the smallest length class analyzed (6–12 mm). Energy content per clam was 78–100% higher in *P. amurensis* than *M. balthica* in the larger two length classes, and 300% higher in the smallest length class that is within the main size eaten by Lesser Scaup in San Francisco Bay (mostly <12 mm).

The force needed to crush shells with a tensometer increased with shell length for both clam species (Fig. 1). However, in accordance with much higher ash content, the thicker shells of *P. amurensis* were harder to crush, and this difference between species increased dramatically with increasing shell length. In the length range of clams eaten by free-ranging Lesser Scaup in San Francisco Bay (mostly <12 mm), the crushing resistance of *P. amurensis* (10.80 $\pm$ 6.61 N; mean $\pm$ 1 SD) was more than nine times greater than that of *M. balthica* (1.15 $\pm$ 0.45 N; $P < 0.001$, Table 1, Fig. 1).

In digestibility trials, variation between clam species in dry mass ingested (Table 2) resulted from species differences in water content of the 25 g fresh mass force-fed to the birds. However, there were no significant differences between clam species in the amounts of dry mass or energy ingested or excreted by the scaup in feeding experiments (t tests, $P > 0.209$, $n = 8$; Table 2). Apparent assimilation efficiency (AE) did not differ between clam species ($P = 0.325$). However, because scaup eating *P. amurensis* lost more body mass (16.0% vs. 11.6%, $P = 0.023$), the usual procedure of adjusting assimilation efficiency for nitrogen balance (AE$_N$) was especially important: mean AE$_N$ was 24% higher for

TABLE 2. Data (mean $\pm$ 1 SD) on scaup body mass before and after feeding experiments; on ingesta and excreta; and on apparent assimilation efficiencies for eight Lesser Scaup fed 25 g fresh mass of the clams *Potamocorbula amurensis* and *Macoma balthica*.

Measurement	*P. amurensis*	*M. balthica*	P†
Body mass			
Initial mass (g)	772 $\pm$ 66	880 $\pm$ 10	0.017
Final mass (g)	648 $\pm$ 54	778 $\pm$ 7	0.003
Mass loss (%)	16.0 $\pm$ 2.7	11.6 $\pm$ 1.2	0.023
Ingesta			
Food, dry mass (g)	16.39 $\pm$ 4.84	12.78 $\pm$ 1.71	0.209
Ash (g)	34.74 $\pm$ 10.26	28.37 $\pm$ 3.79	0.089
Nitrogen (g)	0.07 $\pm$ 0.02	0.10 $\pm$ 0.01	0.034
Energy (kJ)	34.74 $\pm$ 10.26	28.37 $\pm$ 3.79	0.288
Excreta			
Guano (g)	10.66 $\pm$ 3.07	8.69 $\pm$ 1.51	0.293
Ash (g)	9.23 $\pm$ 2.65	7.45 $\pm$ 1.19	0.265
Nitrogen (g)	0.31 $\pm$ 0.13	0.24 $\pm$ 0.05	0.350
Energy (kJ)	16.8 $\pm$ 4.3	15.5 $\pm$ 1.8	0.584
Assimilation‡			
AE (%)	50.5 $\pm$ 7.3	45.0 $\pm$ 7.2	0.325
NB (kJ)	−9.0 $\pm$ 4.7	−5.3 $\pm$ 1.4	0.176
AE$_N$ (%)	78.9 $\pm$ 9.0	63.4 $\pm$ 9.3	0.056

† P values are from t tests between clam species, with percentages being arcsine-transformed before testing.

‡ Calculated apparent assimilation efficiency for energy (AE), nitrogen balance (NB), and AE corrected for nitrogen balance (AE$_N$).
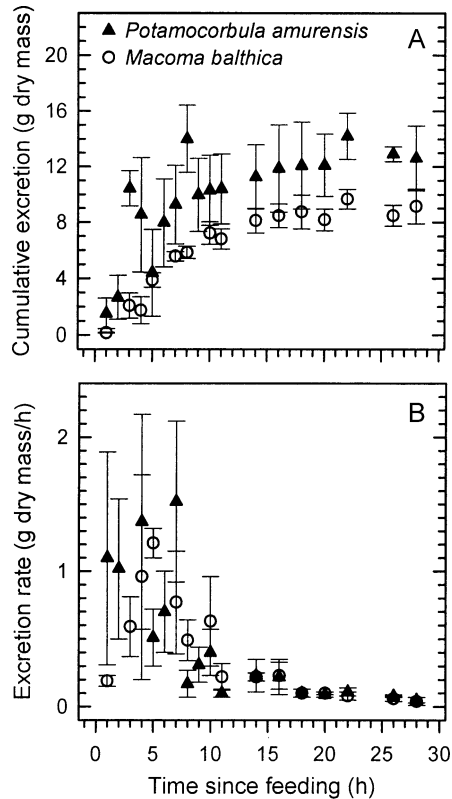
FIG. 2. (A) Cumulative excretion and (B) excretion rate vs. time since feeding for eight Lesser Scaup fed 25 g fresh mass of the clams *Potamocorbula amurensis* or *Macoma balthica*. Error bars show ±1 SE. Because of its higher shell content, values of cumulative excretion were greater for *P. amurensis* (paired t test, $P < 0.001$). 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 3).

P. amurensis ($P = 0.056$). The difference in loss of body mass might have resulted from the differing diets; however, variations of this magnitude are common among ducks confined in experimental cages, owing to differences in activity among individuals (some pace nervously, others mostly sleep; see also Lindgård et al. 1995).

Gut retention times

Because of higher shell content, scaup that were fed *P. amurensis* had greater values of cumulative excretion than those fed *M. balthica* (Fig. 2A). Ducks fed the two species did not differ in excretion rate (Fig. 2B). For *P. amurensis*, estimates of mean retention time in the gut (MRT) increased by 20% when the collection period for calculation was extended from 12 to 18 h, and by another 7% when the collection duration was extended from 18 to 24 h (Table 3). For *M. balthica*, the increases were 18% and 9%. However, MRT did not differ between scaup fed *P. amurensis* and *M. balthica*, regardless of collection duration.

Functional responses

At the same depth in the sediments (3 cm), intake rates were the same for *Potamogeton pectinatus* tubers of different lengths, <6 vs. 6–12 mm ($F_{10,68} = 0.177$, $P > 0.99$; Fig. 3). Data for different lengths were combined in subsequent analyses. For the 3 cm depth, the functional response was $I = 3.752X/(3260 + X)$; $r^2 = 0.92$, $P < 0.001$. However, when tubers were buried an additional 3 cm deeper in the sediments (6 cm), intake rates were much lower ($I = 0.657X/(4018 + X)$; $r^2 = 0.923$, $P < 0.001$. At depths of both 3 cm and 6 cm, intake rates continued to increase with increasing tuber density up to at least 4000 tubers/m^2 (Fig. 3).

For food items <12 mm long buried 3 cm deep, intake rates (number of items per second) by two scaup (one male, one female) feeding on freshly thawed clams (*Nuculana radiata*) at densities of 100, 250, 500, and 1000 clams/m^2 did not differ from those of four scaup feeding on tubers at the same densities ($F_{3,83} = 0.408$, $P = 0.748$). These results indicate that functional responses based on feeding trials with tubers can be extrapolated to freshly thawed clams.

Based on data in Fig. 3 and Tables 1 and 2, functional responses were converted from number of prey consumed per second to ingestion rates of nitrogen (milligrams per second), gross energy (GE, in kilojoules per second), and assimilated energy (GE × assimilation efficiency AE$_N$, in kilojoules per second) for *P. amu-*
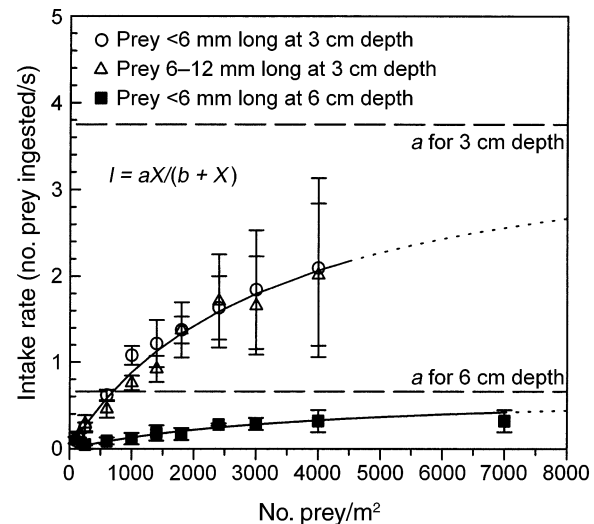

FIG. 3. Functional responses of Lesser Scaup diving 1.8 m to feed on *Potomogeton pectinatus* tubers cut to length (<6 mm and 6–12 mm) at depths in the sediments of 3 cm (four scaup) and 6 cm (three scaup). The model is $I = aX/(b + X)$, where I is the number of prey items ingested per second at the bottom, a is the handling time coefficient or the asymptote for the maximum rate at which scaup can handle prey regardless of prey density, X is the number of prey per square meter, and b is the search time coefficient or the prey density at an intake rate of $0.5a$. Dashed lines are calculated values of a. For fitted parameters and statistics, see *Results: Functional responses*.
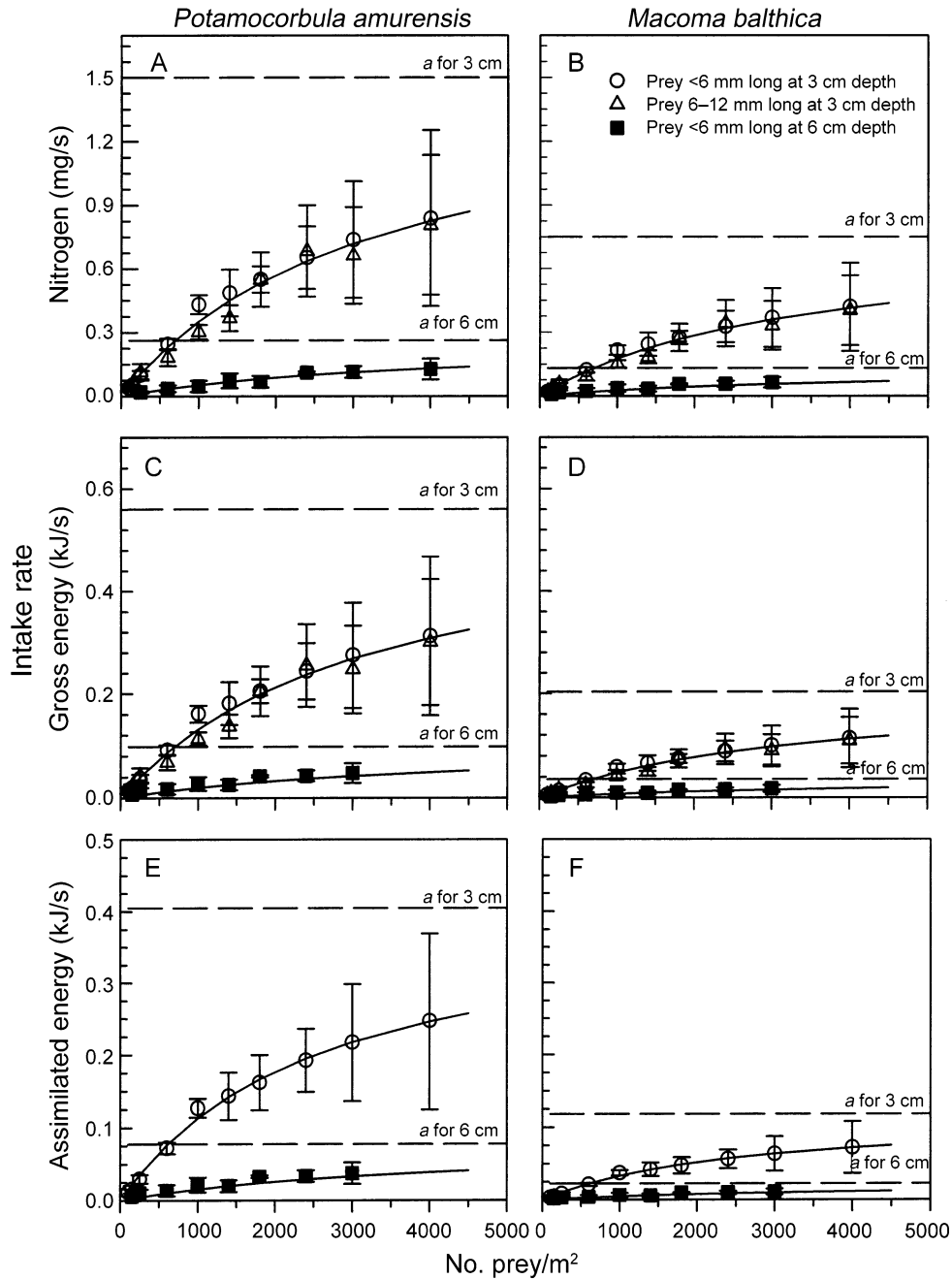
FIG. 4. Calculated functional responses of Lesser Scaup feeding on the clams *Potamocorbula amurensis* and *Macoma balthica* in terms of nitrogen, gross energy (GE), and assimilated energy (GE × assimilation efficiency AE$_N$), based on values in Fig. 3 and Tables 1 and 2. Fitted parameters and statistics are in Table 4. Dashed lines indicate fitted model estimates of the maximum intake rate regardless of prey density (parameter *a* in Table 4) at two depths in the sediments.

rensis and *M. balthica* (Fig. 4, Table 4). Digestibility of protein in flesh has been estimated at ~83% (Zwarts and Blomert 1990); however, we did not measure digestibility of nitrogen for the two species, and did not account for nitrogen assimilation in our calculations of nitrogen intake. Intake of nitrogen, gross energy, and assimilated energy were consistently higher for *P. amu-*

rensis than for *M. balthica* at both 3 cm and 6 cm depths in the sediments (Fig. 4).

DISCUSSION

Since 1986, invasion of San Francisco Bay by the Asian clam *Potamocorbula amurensis* has dramatically altered the prey community of a variety of benthic pred-

TABLE 3.   Mean retention times from mouth to anus (MRT; ± 1 SD) for eight Lesser Scaup fed 25 g fresh mass (including shells) of the clams *Potamocorbula amurensis* and *Macoma balthica*, calculated for collection durations of 12, 18, and 24 h after feeding.

Clam species	Collection duration (h)		
	12	18	24
Potamocorbula amurensis	5.53 $\pm$ 2.07	6.66 $\pm$ 2.93	7.11 $\pm$ 2.92
Macoma balthica	6.30 $\pm$ 1.02	7.44 $\pm$ 0.79	8.13 $\pm$ 0.80

Note: MRT did not differ among collection durations ($P = 0.306$) or between clam species ($P = 0.243$), with no significant interactions ($P = 0.990$) in a two-way ANOVA.

ators, including sharks, rays, sturgeon, flatfish, crabs, and diving ducks (Ganssle 1966, McKechnie and Fenner 1971, Russo 1975, Nichols and Pamatmat 1988, Urquhart and Regalado 1991, Poulton et al. 2002). Impacts on the foraging energetics of these predators have been unknown. Our results show that for a diving duck highly dependent on this habitat, rates of intake and assimilation of nitrogen and energy may be substantially higher for *P. amurensis* than for similar densities and sizes of the once-dominant clam *Macoma balthica*. Although *P. amurensis* has more than twice the ash content of *M. balthica*, the meat content (AFDM) is similar, the nitrogen and energy contents of *P. amurensis* are higher, and its energy content is 24% more digestible (Tables 1 and 2). By these criteria, the exotic *P. amurensis* appears to be a better food than the native *M. balthica*. However, our results suggest two other differences between these species that influence their relative foraging value: resistance of the shell to crushing, and depth in the sediments.

Composition and digestibility of clams

Hard-shelled prey such as clams contain a high fraction of indigestible matter that can restrict available feeding time by limiting storage of food in the digestive tract (Kenward and Sibly 1977, Zwarts and Blomert 1990). The meat of bivalves is highly digestible (Hockey 1984). However, their large bulk of calcium carbonate shell may limit nutrient assimilation by mechanically restricting access of digestive enzymes to the ash-free food 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). In Black Ducks (*Anas rubripes*), Jorde and Owen (1988) found higher digestibility for blue mussels (*Mytilus edulis*) than for soft-shelled clams (*Mya arenaria*) when the ash content of mussels was about ~12% lower. Ash content was 78–100% higher in *P. amurensis* than in *M. balthica* >12 mm long, and three times higher in the shorter length class eaten by scaup in San Francisco Bay (mostly <12 mm). Nevertheless, assimilation efficiency AE_N was 24% higher for *P. amurensis* than for *M. balthica*. Because the nitrogen and lipid fractions of *P. amurensis* and *M. balthica* were not grossly different (Table 1), variations in digestibility between these and other species may be partly explained by differences in the relative fractions of structural and soluble carbohydrates (Beukema and de Bruin 1977, Thompson and Sparks 1978, Zwarts and Blomert 1990).

The $CaCO_3$ in shells can lower measurements of energy content in bomb calorimeters (Paine 1966). However, this effect would reduce the difference in energy content of the two clams (Table 1). The percentage decrease in ash content of excreta vs. ingested clams was similar (~73%) in both species (Table 2). Thus, the greater energy content and higher AE_N measured for *P. amurensis* probably did not result from effects of its greater ash content on bomb calorimetry.

Effects of clam length and depth in the sediments

Larger clams contain more energy per clam, so one might expect ducks to maximize the size of clams in-

TABLE 4.   Fitted parameters of the functional responses in Fig. 4 for Lesser Scaup feeding on the clams *Potamocorbula amurensis* and *Macoma balthica* buried at two depths (3 cm and 6 cm) in the sediments.

Clam species, by depth	Nitrogen (mg/s)			Gross energy (kJ/s)			Assimilated energy (kJ/s)		
	a	*b*	r^2	*a*	*b*	r^2	*a*	*b*	r^2
P. amurensis									
3 cm	1.5006	3260	0.916	0.5605	3260	0.916	0.4048	2585	0.915
6 cm	0.2630	4018	0.923	0.0982	4018	0.924	0.0775	4017	0.923
M. balthica									
3 cm	0.7503	3260	0.916	0.2033	3260	0.916	0.1180	2584	0.915
6 cm	0.1315	4018	0.924	0.0356	4018	0.921	0.0225	4001	0.924

Notes: Model parameters are explained in Fig. 3 (*a*, handling time coefficient or maximum intake rate regardless of prey density; *b*, search time coefficient). All models were significant ($P < 0.001$).

gested. However, in a number of studies, diving ducks have selected clams of intermediate or small length (Draulans 1982, 1984, Bustnes and Erikstad 1990, de Leeuw and van Eerden 1992, Bustnes 1998, Hamilton et al. 1999). In these studies, selection has been explained by differential handling times, effects of meat : shell ratios on nutrient gain relative to passage rate, or as a means of avoiding the risk of ingesting prey that are too large. Although the ash content of *P. amurensis*, which has a thicker shell, was higher than in *M. balthica* of the same length classes, *P. amurensis* had higher energy per clam and higher digestibility. Thus, differences in ash content do not appear to be a key factor in the relative foraging value of the two species.

For Lesser Scaup collected throughout winter 1998–1999 and 1999–2000 in San Francisco Bay, 90% of clams eaten (98% of which were *P. amurensis*) were <12 mm long (J. Y. Takekawa, S. E. Wainwright-De La Cruz, and A. K. Miles, *unpublished data*). At six sites, the shell length of *P. amurensis* was 9.0 ± 1.2 mm (mean ± 1 SE; $n = 111$ clams) in the top 5 cm of sediments, 8.0 ± 0.8 mm ($n = 31$) from 5–10 cm, and 7.6 ± 1.3 mm ($n = 27$) from 10–20 cm depth (1-mm sieve; V. K. Poulton and J. R. Lovvorn, *unpublished data*). For *M. balthica*, shell length was 13.1 ± 1.1 mm ($n = 76$) from 0–5 cm, 18.3 ± 1.2 mm ($n = 54$) from 5–10 cm, and 24.3 ± 2.0 mm ($n = 44$) at 10–20 cm depth in sediments. Thus, even in the top 5 cm of sediments, *M. balthica* was, on average, 64% longer than *P. amurensis* (t test paired by site, $P < 0.001$), and longer than most bivalves eaten by Lesser Scaup here and in the Great Lakes (Custer and Custer 1996). Although the lengths of *P. amurensis* did not increase with depth, lengths of *M. balthica* increased by 40% at 5–10 cm and almost doubled at 10–20 cm depth (Poulton et al. 2002; see also Hines and Comtois 1985). Even for prey <6 mm long, there was a dramatic decrease in intake rates with increased burial depth from 3 to 6 cm (Fig. 3). Thus, *M. balthica* at depths >5 cm were probably not used by Lesser Scaup in 1998–2000 because in those years they were mostly too large and too deep, although the importance of size in addition to depth is difficult to distinguish. At 0–5 cm depth, *M. balthica* and *P. amurensis* are more comparable prey in terms of length and intake rate.

In October–December 1999 in northern San Francisco Bay (San Pablo and San Quentin Bays), the mean density (number of individuals per square meter) in the top 20 cm at six sites was 243.4 (range 36.2–657.7 among sites) for *P. amurensis* vs. 52.8 (range 0–112.7) for *M. balthica* (1-mm sieve; Poulton 2002). However, the top 5 cm of sediments contained 97% of *P. amurensis* but only 48% of *M. balthica* (Poulton et al. 2002), so mean densities in the top 5 cm were ~236 clams/m² for *P. amurensis* vs. 25 clams/m² for *M. balthica*. Thus, at population levels in late fall 1999, *P. amurensis* was 9–10 times more available than *M. balthica* of suitable sizes and shallow depths. Although data are lacking from a range of sites, it is likely that *P. amurensis* achieves higher overall densities than did *M. balthica* before *P. amurensis* invaded (Nichols and Thompson 1985, Carlton et al. 1990, Nichols et al. 1990). However, even at the same population densities, numbers of clams of suitable size in the top 5 cm of sediments would be twice as high for *P. amurensis* as for *M. balthica*. In addition to nutrient and energy content and digestibility, it appears that *P. amurensis* is a better food than *M. balthica* in terms of both length frequencies and burial depth.

Effects of clam size and burial depth may differ for other benthic predators. In analogous captive studies of the White-winged Scoter (*Melanitta fusca*), whose close congener the Surf Scoter (*M. perspicillata*) is very abundant in San Francisco Bay (Accurso 1992), intake rate of freshly thawed *M. balthica* 18–24 mm long was limited by clam density up to at least 2000 clams/m², whereas intake of *M. balthica* 24–30 mm long was more limited by handling time at densities >400 clams/m². For the smaller length class (18–24 mm), increasing burial depth from 4 to 7 cm reduced intake rate for these much larger ducks by 31% (Richman and Lovvorn 2003). We are aware of no data on the functional responses of fish feeding on benthos, especially as affected by size or burial depth of prey. However, Dungeness crabs (*Cancer magister*) show strong size selection (Juanes and Hartwick 1990); and although adult blue crabs (*Callinectes sapidus*) readily prey on *M. balthica* at sediment depths well below 5 cm, intake rates decline with increasing prey depth (Blundon and Kennedy 1982, Lipcius and Hines 1986, Seitz et al. 2001).

Crushing resistance of shells

Although the much higher ash content of *P. amurensis* did not reduce its digestibility relative to *M. balthica*, the thicker shell of *P. amurensis* made its resistance to crushing far greater. Even in the range of clam lengths eaten by Lesser Scaup in San Francisco Bay (mostly <12 mm), this factor might appreciably offset the other foraging advantages of *P. amurensis* over *M. balthica*. We have no measure of the actual costs to Lesser Scaup of crushing these clams in the gizzard. In Tufted Ducks (*Aythya fuligula*), a congener similar in size to Lesser Scaup, de Leeuw et al. (1998) suggested that energy required to crush the shells of zebra mussels (*Dreissena polymorpha*) was a significant part of the energy budget. However, they also suggested that heat so produced could substitute for thermogenesis, thereby reducing the cost of thermoregulation. Such effects might be addressed by comparing the oxygen consumption of Lesser Scaup fed on the two clam species while diving under controlled conditions at temperatures and depths found in San Francisco Bay (cf., Kaseloo 2002), but any differences in crushing costs would be difficult to detect.

Gizzard mass (and crushing strength) are highly adaptable over periods of 6–10 days, with gizzard mass increasing by 30–80% in response to increased demand (Kehoe et al. 1988, Piersma et al. 1993, Dekinga et al. 2001). Thus, it is unlikely that the higher crushing resistance of *P. amurensis* constrains intake or processing rates over winter. However, greater shell strength may reduce energetic profitability (gain minus cost) by increasing the costs of crushing clams or of maintaining larger gizzards.

Gut retention times

For free-ranging scaup and other benthic-feeding diving ducks, resting periods between dive bouts (usually <15 min) are far less than the mean gut retention times of ≥5 h for scaup eating clams in this study (Table 3; see Guillemette 1994, 1998; J. R. Lovvorn, *unpublished data*). It appears that scaup often resume feeding long before the bulk of food ingested during the previous dive bout has exited the gut. Although methods vary widely, our values for mean retention time are in the range (3–7 h) of those reported for ducks and geese eating hard plant foods, and for seabirds eating fish (Halse 1984, Takekawa 1987, Hilton et al. 1998). It is unknown whether grinding in the gizzard proceeds during feeding, or if grinding begins only after a dive bout is completed (Guillemette 1994). For Mallards (*Anas platyrhynchos*) eating 25-g meals of grains, mean retention times were ~5 h, but the esophagus–proventriculus was emptied in 15–45 min (Clark and Gentle 1990). Retrograde movement of portions of digesta (Clemens et al. 1975) may retain some fractions while others pass more rapidly, and some shell material may stay in the gizzard longer. Such effects might inflate retention time for the entire meal beyond the time needed for the esophagus–proventriculus to clear for further feeding. Chemical reactor theory has been used to discriminate the time digesta spend in the "stomach" (esophagus, proventriculus, and gizzard) from time spent in the intestines (Karasov and Cork 1996, Hilton et al. 2000), but our data violated assumptions of this theory, resulting in unrealistic model estimates. In summary, time required to clear the esophagus–proventriculus may limit intake rate by scaup over short periods, but intake rate does not seem to be directly constrained by mean retention time.

More important to questions in this paper is the lack of difference in mean retention time (MRT) between *P. amurensis* and *M. balthica* (Fig. 2, Table 3). Size of meals can have either negligible or significant effects on MRT depending on bird species, food type, and possibly experimental conditions (Dykstra and Karasov 1992, Jackson 1992, Hilton et al. 1998), but our scaup were fed the same fresh mass of the two clam species. If the sum of time spent foraging and time spent digesting is less than the total time available for foraging, then MRT does not limit nutrient acquisition. If the sum of time spent foraging and digesting exceeds time available for foraging, MRT may limit nutrient acquisition, but is still unimportant to the *relative* foraging value of these two clam species with similar MRT. Digestive processing time may be longer than the time needed to fill the gut (Jeschke et al. 2002), but the cost of diving to a depth of 2 m is at least 2.6–4.3 times higher than floating on the surface while digesting food (Kaseloo 2002). Thus, given the similar MRT for these clam species, the key determinant of their relative profitability (gain minus cost) is the intake rate of digestible nutrients during short, costly dives. Because the intake rates of nitrogen and energy were higher for *P. amurensis* than *M. balthica* at all clam densities that we studied (Fig. 4), *P. amurensis* is a better food, regardless of whether or not energy acquisition is limited by digestive processing time.

Contaminant exposure

Potamocorbula amurensis filters water at high rates and is believed to be responsible for dramatic reductions in phytoplankton and zooplankton biomass in northern San Francisco Bay (Alpine and Cloern 1992, Cole et al. 1992, Kimmerer et al. 1994). Partly for the same reason, *P. amurensis* also accumulates high concentrations of selenium, hydrocarbons, and some heavy metals (Pereira et al. 1992, Brown and Luoma 1995, Linville et al. 2002). Selenium concentrations in *P. amurensis* in northern San Francisco Bay (San Pablo and Suisun Bays) were three times higher in 1995–1997 than in earlier studies, and 1990 concentrations in sturgeon and diving ducks were also higher than in 1986, before the tremendous increase of *P. amurensis* (Linville et al. 2002). In 1988, concentrations (ppm) of Se in scaup liver were 12 μg Se/g dry mass in San Pablo Bay compared to 3.4 μg Se/g at a control site in Humboldt Bay (White et al. 1989). In June 1997 in Carquinez Stait (just upstream from San Pablo Bay), *P. amurensis* had a selenium concentration (mean ± 1 SD) of 12.9 ± 1.2 μg Se/g dry mass, whereas *M. balthica* contained only 3.7 ± 0.1 μg Se/g dry mass (Linville et al. 2002). Thus, exposure of benthic predators to some contaminants has been substantially increased by invasion of *P. amurensis* and displacement of native species. Similar effects have occurred for organochlorine contaminants in diving ducks eating exotic zebra mussels in the Great Lakes (Mazak et al. 1997).

Scaup diet before P. amurensis *invaded*

During winter 1998–1999 and 1999–2000, *P. amurensis* comprised 96% of the dry mass of the esophagus contents of 13 Lesser Scaup collected in San Pablo Bay (J. Y. Takekawa, S. E. Wainwright-De La Cruz, and A. K. Miles, *unpublished data*). Only one of these birds contained one *M. balthica* clam, although *M. balthica* was common in the area (Poulton et al. 2002). The diet of scaup in San Francisco Bay before 1986 is unknown. However, we speculate that small *M. balthica*, a common food of scaup in other wintering areas (Madsen

1954, Yocom and Keller 1961, Stewart 1962, Nilsson 1972, Perry and Uhler 1982), and *Gemma gemma*, once abundant but not found in San Pablo Bay in winter 1999–2000 (Thompson 1982, Poulton et al. 2004), were important foods. *Gemma gemma* is small (mostly <3 mm long), reaches high densities, and is distributed near the sediment surface like *P. amurensis* (Vassallo 1971, Thompson 1982). However, because *M. balthica* is distributed over a greater range of burial depths, its population size would have to be much larger to maintain similar numbers of younger clams at the shallow burial depths exploited by Lesser Scaup.

Conclusions

The exotic clam *Potamocorbula amurensis* has higher nitrogen and energy content, and higher digestibility of energy for Lesser Scaup, than does the native and formerly dominant clam *Macoma balthica*. Gut retention times by scaup do not differ between the clam species, and the much higher cost of diving than of digesting food at the water surface makes their relative profitability more dependent on intake rates while the bird is underwater. A much higher fraction of *P. amurensis* is in the length range most commonly eaten by Lesser Scaup, and almost all are distributed in the top 5 cm of sediments where scaup intake rates are highest. The thicker shell of *P. amurensis* does not decrease its digestibility relative to *M. balthica*, but requires much more energy to crush. The latter factor might partly offset the apparent energetic advantages of *P. amurensis*, but net effects including thermal substitution of heat produced by gizzard action need to be assessed. In many respects, *P. amurensis* appears to be a more valuable food than *M. balthica*, but its greater concentration of some contaminants has increased the risk of toxicity to a range of benthic predators. Thus, invasion of *P. amurensis*, while having dramatic negative effects on preexisting benthic communities, has had mixed effects on benthic predators like Lesser Scaup.

LITERATURE CITED

Accurso, L. M. 1992. Distribution and abundance of wintering waterfowl on San Francisco Bay. Thesis. Humboldt State University, Humboldt, California, USA.

Alpine, A. E., and J. E. Cloern. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. Limnology and Oceanography **37**:946–955.

Ansell, A. D. 1995. Surface activity of some benthic invertebrate prey in relation to the foraging activity of juvenile flatfishes. Pages 245–252 *in* A. Eleftheriou, A. D. Ansell, and C. J. Smith, editors. Biology and ecology of shallow coastal waters. Proceedings of the 28th Marine Biology Symposium. Olsen and Olsen, Fredensborg, Denmark.

Austin, J. E., A. D. Afton, M. G. Anderson, R. G. Clark, C. M. Custer, J. S. Lawrence, J. B. Pollard, and J. K. Ringelman. 2000. Declining scaup populations: issues, hypotheses, and research needs. Wildlife Society Bulletin **28**:254–263.

Baldwin, J. R., and J. R. Lovvorn. 1994. Major expansion of seagrass habitat by the exotic *Zostera japonica*, and its use by dabbling ducks and Brant in Boundary Bay, British Columbia. Marine Ecology Progress Series **103**:199–127.

Ball, J. P. 1994. Prey choice of omnivorous Canvasbacks: imperfectly optimal ducks? Oikos **70**:233–244.

Beauchamp, G., M. Guillemette, and R. Ydenberg. 1992. Prey selection while diving by Common Eiders, *Somateria mollissima*. Animal Behaviour **44**:417–426.

Bellrose, F. C. 1980. Ducks, geese and swans of North America. Stackpole Books, Harrisburg, Pennsylvania, USA.

Beukema, J. J., and W. de Bruin. 1977. Seasonal changes in dry weight and chemical composition of the soft parts of the tellenid bivalve *Macoma balthica* in the Dutch Wadden Sea. Netherlands Journal of Sea Research **11**:42–55.

Blundon, J. A., and V. S. Kennedy. 1982. Refuges for infaunal bivalves from blue crab, *Callinectes sapidus* (Rathbun), predation in Chesapeake Bay. Journal of Experimental Marine Biology and Ecology **65**:67–81.

Brown, C. L., and S. N. Luoma. 1995. Use of the euryhaline bivalve *Potamocorbula amurensis* as a biosentinel species to assess trace metal contamination in San Francisco Bay. Marine Ecology Progress Series **124**:129–142.

Bustnes, J. O. 1998. Selection of blue mussels, *Mytilus edulis*, by Common Eiders, *Somateria mollissima*, by size in relation to shell content. Canadian Journal of Zoology **76**:1787–1790.

Bustnes, J. O., and K. E. Erikstad. 1990. Size selection of common mussels, *Mytilus edulis*, by Common Eiders, *Somateria mollissima*: energy maximization or shell weight minimization? Canadian Journal of Zoology **68**:2280–2283.

Carbone, C. 1995. Guidelines for estimating the feeding performance of diving birds. Wildfowl **46**:119–128.

Carlton, J. T., J. K. Thompson, L. E. Schemel, and F. N. Nichols. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis*. I. Introduction and dispersal. Marine Ecology Progress Series **66**:81–94.

Chatterjee, S., A. S. Hadi, and B. Price. 2000. Regression analysis by example. John Wiley, New York, New York, USA.

Clark, R. G., and G. C. Gentle. 1990. Estimates of grain passage time in captive Mallards. Canadian Journal of Zoology **68**:2275–2279.

Clemens, E. T., C. E. Stevens, and M. Southworth. 1975. Sites of organic acid production and pattern of digesta movement in the gastrointestinal tract of geese. Journal of Nutrition **105**:1341–1350.

Cohen, A. N., and J. T. Carlton. 1998. Accelerating invasion rate in a highly invaded estuary. Science **279**:555–558.

Cole, B. E., J. K. Thompson, and J. E. Cloern. 1992. Measurement of filtration rates by infaunal bivalves in a recirculating flume. Marine Biology **113**:219–225.

Custer, C. M., and T. W. Custer. 1996. Food habits of diving ducks in the Great Lakes after the zebra mussel invasion. Journal of Field Ornithology **67**:86–99.

Dekinga, A., M. W. Dietz, A. Koolhaas, and T. Piersma. 2001. Time course and reversibility of changes in the gizzards of

Red Knots alternatively eating hard and soft food. Journal of Experimental Biology **204**:2167–2173.

de Leeuw, J. J., P. J. Butler, A. J. Woakes, and F. Zegwaard. 1998. Body cooling and its energetic implications for feeding and diving of Tufted Ducks. Physiological Zoology **71**:720–730.

de Leeuw, J. J., and M. R. van Eerden. 1992. Size selection in diving Tufted Ducks *Aythya fuligula* explained by differential handling of small and large mussels *Dreissena polymorpha*. Ardea **80**:353–362.

Draulans, D. 1982. Foraging and size selection of mussels by the Tufted Duck, *Aythya fuligula*. Journal of Animal Ecology **51**:943–956.

Draulans, D. 1984. Sub-optimal mussel selection by Tufted Ducks *Aythya fuligula*: test of a hypothesis. Animal Behaviour **32**:1192–1196.

Draulans, D. 1987. The effect of prey density on foraging behaviour and success of adult and first-year Grey Herons (*Ardea cinerea*). Journal of Animal Ecology **56**:479–493.

Dykstra, C. R., and W. H. Karasov. 1992. Changes in gut structure and function of House Wrens (*Troglodytes aedon*) in response to increased energy demands. Physiological Zoology **65**:422–442.

Evans, P. R. 1979. Adaptations shown by foraging shorebirds to cyclical variations in the activity and availability of their intertidal invertebrate prey. Pages 357–366 *in* E. Naylor and R. G. Hartnoll, editors. Cyclic phenomena in marine plants and animals. Pergamon Press, Oxford, UK.

French, J. R. P. 1993. How well can fishes prey on zebra mussels in eastern North America? Fisheries **18**:13–19.

French, J. R. P., and M. T. Bur. 1996. The effect of zebra mussel consumption on growth of freshwater drum in Lake Erie. Journal of Freshwater Ecology **11**:283–289.

Ganssle, D. 1966. Fishes and decapods of San Pablo and Suisun Bays. Fish Bulletin **133**:64–94.

Giles, N. 1990. Effects of increasing larval chironomid densities on the underwater feeding success of downy Tufted ducklings *Aythya fuligula*. Wildfowl **41**:99–106.

Goede, A. A., H. T. Wolterbeek, and M. J. Koese. 1993. Selenium concentrations in the marine invertebrates *Macoma balthica*, *Mytilus edulis*, and *Nereis diversicolor*. Archives of Environmental Contamination and Toxicology **25**:85–89.

Guillemette, M. 1994. Digestive-rate constraint in wintering Common Eiders (*Somateria mollissima*): implications for flying capabilities. Auk **111**:900–909.

Guillemette, M. 1998. The effect of time and digestion constraints in Common Eiders while feeding and diving over blue mussel beds. Functional Ecology **12**:123–131.

Halse, S. A. 1984. Food intake, digestive efficiency and retention time in Spur-winged Geese *Plectropterus gambensis*. South African Journal of Wildlife Research **14**:106–110.

Hamilton, D. J., C. D. Ankney, and R. C. Bailey. 1994. Predation of zebra mussels by diving ducks: an exclosure study. Ecology **75**:521–531.

Hamilton, D. J., T. D. Nudds, and J. Neate. 1999. Size-selective predation of blue mussels (*Mytilus edulis*) by Common Eiders (*Somateria mollissima*) under controlled field conditions. Auk **116**:403–416.

Hilton, G. M., R. W. Furness, and D. C. Houston. 2000. A comparative study of digestion in North Atlantic seabirds. Journal of Avian Biology **31**:36–46.

Hilton, G. M., D. C. Houston, and R. W. Furness. 1998. Which components of diet quality affect retention time of digesta in seabirds? Functional Ecology **12**:929–939.

Hines, A. H., and K. L. Comtois. 1985. Vertical distribution of infauna in sediments of a subestuary of central Chesapeake Bay. Estuaries **8**:296–304.

Hockey, P. A. R. 1984. Growth and energetics of the African Black Oystercatcher *Haematopus moquini*. Ardea **72**:111–117.

Hothem, R. L., D. G. Lonzarich, J. E. Takekawa, and H. M. Ohlendorf. 1998. Contaminants in wintering Canvasbacks and scaups from San Francisco Bay, California. Environmental Monitoring and Assessment **50**:67–84.

Jackson, S. 1992. Do seabird gut sizes and mean retention times reflect adaptation to diet and foraging methods? Physiological Zoology **65**:674–697.

Jeschke, J. M., M. Kopp, and R. Tollrian. 2002. Predator functional responses: discriminating between handling and digesting prey. Ecological Monographs **72**:95–112.

Jorde, D. G., and R. B. Owen. 1988. Efficiency of nutrient use by American Black Ducks wintering in Maine. Journal of Wildlife Management **52**:209–214.

Juanes, F., and E. B. Hartwick. 1990. Prey size selection in Dungeness crabs: the effect of claw damage. Ecology **71**:744–758.

Kaiser, M. J., A. P. Westhead, R. N. Hughes, and R. N. Gibson. 1992. Are digestive characteristics important contributors to the profitability of prey? Oecologia **90**:61–69.

Karasov, W. H., and S. J. Cork. 1996. Test of a reactor-based digestion optimization model for nectar-eating Rainbow Lorikeets. Physiological Zoology **69**:117–138.

Kaseloo, P. A. 2002. Thermal substitution from the heat increment of feeding and activity in dabbling and diving ducks. Dissertation. University of Wyoming, Laramie, Wyoming, USA.

Kehoe, F. P., C. D. Ankney, and R. T. Alisauskas. 1988. Effects of dietary fiber and diet diversity on digestive organs of captive Mallards (*Anas platyrhynchos*). Canadian Journal of Zoology **66**:1597–1602.

Kenward, R. E., and R. M. Sibly. 1977. A Woodpigeon (*Columba palumbus*) feeding preference explained by a digestive bottleneck. Journal of Applied Ecology **14**:815–826.

Kimmerer, W. J., E. Gartside, and J. J. Orsi. 1994. Predation by an introduced clam as the likely cause of substantial declines in zooplankton of San Francisco Bay. Marine Ecology Pregress Series **113**:81–93.

Kirkwood, R., and G. Robertson. 1997. The energy assimilation efficiency of Emperor Penguins, *Aptenodytes forsteri*, fed a diet of Antarctic krill, *Euphausia superba*. Physiological Zoology **70**:27–32.

Kolar, C. S., and D. M. Lodge. 2000. Freshwater nonindigenous species: interactions with other global changes. Pages 3–30 *in* H. A. Mooney and R. J. Hobbs, editors. Invasive species in a changing world. Island Press, Washington, D.C., USA.

Lindgård, K., S. Näslund, and K. A. Stokkan. 1995. Annual changes in body mass in captive Svalbard Ptarmigan: role of changes in locomotor activity and food intake. Journal of Comparative Physiology B **165**:445–449.

Linville, R. G., S. N. Luoma, L. Cutter, and G. A. Cutter. 2002. Increased selenium threat as a result of invasion of the exotic bivalve *Potamocorbula amurensis* in the San Francisco Bay-Delta. Aquatic Toxicology **57**:51–64.

Lipcius, R. N., and A. H. Hines. 1986. Variable functional responses of a marine predator in dissimilar homogeneous microhabitats. Ecology **67**:1361–1371.

Lovvorn, J. R. 1994. Biomechanics and foraging profitability: an approach to assessing trophic needs and impacts of diving ducks. Hydrobiologia **279/280**:223–233.

Lovvorn, J. R., and M. P. Gillingham. 1996*a*. A spatial energetics model of cadmium accumulation by diving ducks. Archives of Environmental Contamination and Toxicology **30**:241–251.

Lovvorn, J. R., and M. P. Gillingham. 1996*b*. Food dispersion and foraging energetics: a mechanistic synthesis for field studies of avian benthivores. Ecology **77**:435–451.

Lovvorn, J. R., and D. R. Jones. 1991. Effects of body size, body fat, and change in pressure with depth on buoyancy and costs of diving in ducks. Canadian Journal of Zoology **69**:2879–2887.

Lovvorn, J. R., D. R. Jones, and R. W. Blake. 1991. Mechanics of underwater locomotion in diving ducks: drag, buoyancy and acceleration in a size gradient of species. Journal of Experimental Biology **159**:89–108.

Ludyanskiy, M. L., D. McDonald, and D. MacNeill. 1993. Impact of the zebra mussel, a bivalve invader. BioScience **43**:533–544.

Madsen, J. F. 1954. On the food habits of the diving ducks in Denmark. Danish Review of Game Biology **2**:157–266.

Mazak, E. J., H. J. MacIsaac, M. R. Servos, and R. Hesslein. 1997. Influence of feeding habits on organochlorine contaminant accumulation in waterfowl on the Great Lakes. Ecological Applications **7**:1133–1143.

McKechnie, R. J., and R. B. Fenner. 1971. Food habits of white sturgeon, *Acipenser transmontanus*, in San Pablo and Suisun Bays, California. California Fish and Game **57**:209–212.

Myers, J. P., S. L. Williams, and F. A. Pitelka. 1980. An experimental analysis of prey availability for Sanderlings (Aves: Scolopacidae) feeding on sandy beach crustaceans. Canadian Journal of Zoology **58**:1564–1574.

Navarro, R. A., C. R. Velasquez, and R. P. Schlatter. 1989. Diet of the Surfbird in southern Chile. Wilson Bulletin **101**:137–141.

Nichols, F. H., and M. M. Pamatmat. 1988. The ecology of the soft-bottom benthos of San Francisco Bay: a community profile. U.S. Fish and Wildlife Service Biological Report **85**(**7.23**).

Nichols, F. H., and J. K. Thompson. 1985. Time scales of change in the San Francisco Bay benthos. Hydrobiologia **129**:121–138.

Nichols, F. H., J. K. Thompson, and L. E. Schemel. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis*. II. Displacement of a former community. Marine Ecology Progress Series **66**:95–101.

Nilsson, L. 1972. Habitat selection, food choice, and feeding habits of diving ducks in coastal waters of South Sweden during the non-breeding season. Ornis Scandinavica **3**:55–78.

Ohlendorf, H. M., R. W. Lowe, P. R. Kelly, and T. E. Harvey. 1986. Selenium and heavy metals in San Francisco Bay diving ducks. Journal of Wildlife Management **50**:64–71.

Paine, R. T. 1966. Endothermy in bomb calorimetry. Limnology and Oceanography **11**:126–129.

Pereira, W. E., F. D. Hostettler, and J. B. Rapp. 1992. Bioaccumulation of hydrocarbons derived from terrestrial and anthropogenic sources in the Asian clam, *Potamocorbula amurensis*, in San Francisco Bay Estuary. Marine Pollution Bulletin **24**:103–109.

Perry, M. C., and F. M. Uhler. 1981. Asiatic clam (*Corbicula manilensis*) and other foods used by waterfowl in the James River, Virginia. Estuaries **4**:229–233.

Perry, M. C., and F. M. Uhler. 1982. Food habits of diving ducks in the Carolinas. Proceedings of the Annual Conference of the Southeast Association of Fish and Wildlife Agencies **36**:492–504.

Peterson, C. H., and M. L. Quammen. 1982. Siphon nipping: its importance to small fishes and its impact on growth of the bivalve *Protothaca staminea* (Conrad). Journal of Experimental Marine Biology and Ecology **63**:249–268.

Peterson, C. H., and G. A. Skilleter. 1994. Control of foraging behavior of individuals within an ecosystem context: the clam *Macoma balthica*, flow environment, and siphon-cropping fishes. Oecologia **100**:256–267.

Piersma, T., A. Koolhaas, and A. Dekinga. 1993. Interactions between stomach structure and diet choice in shorebirds. Auk **110**:552–564.

Piersma, T., J. van Gils, P. de Goeij, and J. van der Meer. 1995. Holling's functional response model as a tool to link the food-finding mechanism of a probing shorebird with its spatial distribution. Journal of Animal Ecology **64**:493–504.

Posey, M. H. 1988. Community changes associated with the spread of an introduced seagrass, *Zostera japonica*. Ecology **69**:974–983.

Poulton, V. K. 2002. Behavior of scaup ducks relative to seasonal abundance and dispersion of their benthic prey in San Pablo Bay, California. Thesis. University of Wyoming, Laramie, Wyoming, USA.

Poulton, V. K., J. R. Lovvorn, and J. Y. Takekawa. 2002. Clam density and scaup feeding behavior in San Pablo Bay, California. Condor **104**:518–527.

Poulton, V. K., J. R. Lovvorn, and J. Y. Takekawa. 2004. Spatial and overwinter changes in clam populations of San Pablo Bay, a semiarid estuary with highly variable freshwater inflow. Estuarine, Coastal and Shelf Science **59**:459–473.

Reading, C. J., and S. McGrorty. 1978. Seasonal variations in the burying depth of *Macoma balthica* (L.) and its accessibility to wading birds. Estuarine and Coastal Marine Science **6**:135–144.

Richman, S. E., and J. R. Lovvorn. 2003. Effects of clam species dominance on nutrient and energy acquisition by Spectacled Eiders in the Bering Sea. Marine Ecology Progress Series **261**:283–297.

Russo, R. A. 1975. Observations on the food habits of leopard sharks (*Triakis semifasciata*) and brown smoothhounds (*Mustelus henlei*). California Fish and Game **61**:95–103.

SAS Institute. 1987. SAS/STAT guide for personal computers. SAS Institute, Cary, North Carolina, USA.

Seitz, R. D., R. N. Lipcius, A. H. Hines, and D. B. Eggleston. 2001. Density-dependent predation, habitat variation, and the persistence of marine bivalve prey. Ecology **82**:2435–2451.

Sibbald, I. R. 1979. Passage of feed through the adult rooster. Poultry Science **58**:446–459.

Sibbald, I. R. 1982. Measurement of bioavailable energy in poultry feeding stuffs: a review. Canadian Journal of Animal Science **62**:983–1048.

Skilleter, G. A., and C. H. Peterson. 1994. Control of foraging behavior of individuals within an ecosystem context: the clam *Macoma balthica* and interactions between competition and siphon cropping. Oecologia **100**:268–278.

Skorupa, J. P., and H. M. Ohlendorf. 1991. Contaminants in drainage water and avian risk thresholds. Pages 345–368 *in* A. Dinar and D. Zilberman, editors. The economics and management of water and drainage in agriculture. Kluwer Academic, Boston, Massachusetts, USA.

Speakman, J. R. 1987. Apparent absorption efficiencies for Redshank (*Tringa totanus* L.) and Oystercatchers (*Haematopus ostralegus* L.): implications for the predictions of optimal foraging models. American Naturalist **130**:677–691.

Stanley, S. M. 1970. Relation of shell form to life habits of the Bivalvia (Mollusca). Geological Society of America Memoir **125**.

Stephenson, R. 1994. Diving energetics of Lesser Scaup (*Aythya affinis*, Eyton). Journal of Experimental Biology **190**:155–178.

Stewart, R. E. 1962. Waterfowl populations in the upper Chesapeake region. U.S. Fish and Wildlife Service Special Scientific Report, Wildlife **65**.

Stewart, T. W., and J. M. Haynes. 1994. Benthic macroinvertebrate communities of southwestern Lake Ontario fol-

lowing invasion of *Dreissena*. Journal of Great Lakes Research **20**:479–493.

Strong, C. R., and S. N. Luoma. 1981. Variations in the correlation of body size with concentrations of Cu and Ag in the bivalve *Macoma balthica*. Canadian Journal of Fisheries and Aquatic Sciences **38**:1059–1064.

Takekawa, J. Y. 1987. Energetics of Canvasbacks staging on an upper Mississippi River pool during fall migration. Dissertation. Iowa State University, Ames, Iowa, USA.

Tallqvist, M. 2001. Burrowing behaviour of the Baltic clam *Macoma balthica*: effects of sediment type, hypoxia and predator presence. Marine Ecology Progress Series **212**: 183–191.

Thompson, C. M., and R. E. Sparks. 1978. Comparative nutritional value of a native fingernail clam and the introduced Asiatic clam. Journal of Wildlife Management **42**:391–396.

Thompson, J. K. 1982. Population structure of *Gemma gemma* (Bivalvia: Veridae) in south San Francisco Bay, with a comparison to some northeastern United States estuarine populations. Veliger **24**:281–290.

Titus, H. W., A. L. Mehring, D. Johnson, L. L. Nesbitt, Jr., and T. Tomas. 1959. An evaluation of MCF (Micro-Cel-Fat), a new type of fat product. Poultry Science **38**:1114–1119.

Urquhart, K. A. F., and K. Regalado. 1991. Selenium verification study, 1988–1990. California Water Resources Control Board 91-2-WQ, Sacramento, California, USA.

Vassallo, M. T. 1971. The ecology of *Macoma inconspicua* (Broderip & Sowerby, 1829) in central San Francisco Bay. Part II. Stratification of the *Macoma* community within the substrate. Veliger **13**:279–284.

Wanink, J., and L. Zwarts. 1985. Does an optimally foraging oystercatcher obey the functional response? Oecologia **67**: 98–106.

White, J. R., P. S. Hofmann, K. A. F. Urquhart, D. Hammond, and S. Baumgartner. 1989. Selenium verification study 1987–1988. A report to the State Water Resources Control Board. California Department of Fish and Game, Sacramento, California, USA.

Yocom, C. F., and M. Keller. 1961. Correlation of food habits and abundance of waterfowl, Humboldt Bay, California. California Fish and Game **47**:41–53.

Zwarts, L., and A. Blomert. 1990. Selectivity of Whimbrels feeding on fiddler crabs explained by component specific digestibilities. Ardea **78**:193–208.

Zwarts, L., and A. Blomert. 1992. Why Knot *Calidris canutus* take medium-sized *Macoma balthica* when six prey species are available. Marine Ecology Progress Series **83**:113–128.

Zwarts, L., A. Blomert, and J. H. Wanink. 1992. Annual and seasonal variation in the food supply harvestable by Knot *Calidris canutus* staging in the Wadden Sea in late summer. Marine Ecology Progress Series **83**:129–139.