CLAM DENSITY AND SCAUP FEEDING BEHAVIOR IN SAN PABLO BAY, CALIFORNIA

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Abstract. San Pablo Bay, in northern San Francisco Bay, California, is an important wintering area for Greater (*Aythya marila*) and Lesser Scaup (*A. affinis*). We investigated variation in foraging behavior of scaup among five sites in San Pablo Bay, and whether such variation was related to densities of their main potential prey, the clams *Potamocorbula amurensis* and *Macoma balthica*. Time-activity budgets showed that scaup spent most of their time sleeping at some sites, and both sleeping and feeding at other sites, with females feeding more than males. In the first half of the observation period (12 January–5 February 2000), percent time spent feeding increased with increasing density of *P. amurensis*, but decreased with increasing density of *M. balthica* (diet studies have shown that scaup ate mostly *P. amurensis* and little or no *M. balthica*). Densities of *M. balthica* stayed about the same between fall and spring benthic samples, while densities of *P. amurensis* declined dramatically at most sites. In the second half of the observation period (7 February–3 March 2000), percent time feeding was no longer strongly related to *P. amurensis* densities, and dive durations increased by 14%. These changes probably reflected declines of *P. amurensis*, perhaps as affected by scaup predation. The large area of potential feeding habitat, and alternative prey elsewhere in the estuary, might have resulted in the low correlations between scaup behavior and prey densities in San Pablo Bay. These low correlations made it difficult to identify specific areas of prey concentrations important to scaup.

Key words: Aythya affinis, Aythya marila, clam densities, Macoma balthica, Potamocorbula amurensis, San Francisco Bay, scaup feeding behavior.

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INTRODUCTION

San Francisco Bay supports peak numbers of up to 284 000 waterfowl during winter. Greater (*Aythya marila*) and Lesser Scaup (*A. affinis*) make up 43–46% of this total, and up to 92% of scaup in the Pacific Flyway may be in San Francisco Bay at one time (Accurso 1992). Most of these scaup use San Pablo Bay in northern San Francisco Bay, where they eat clams and other benthic macroinvertebrates. Scaup populations have decreased on some nesting areas in North America (Austin et al. 2000), and on wintering areas in San Francisco Bay and Puget Sound (Nysewander and Evenson 1998). However, it is unclear whether prey quality, quantity, and habitat characteristics on wintering areas might be contributing to these declines.

Availability of prey to benthic feeders in San Pablo Bay changes with freshwater inflow from the Sacramento-San Joaquin estuary. Increased freshwater inflow during winter and spring, and wind-generated turbulence in summer, result in an invertebrate community with low species richness and wide fluctuations in density (Nichols and Thompson 1985b). The native clam *Macoma balthica* and the introduced Asian clam *Potamocorbula amurensis* are the most abundant potential foods for scaup in San Pablo Bay. *M. balthica* has been an important food for both Lesser and Greater Scaup wintering elsewhere in North America and Europe (Yocom and Keller 1961, Stewart 1962, Nilsson 1972, Perry and Uhler 1982). However, in winter 1999–2000, *P. amurensis* was the main food of Lesser Scaup and an important food of Greater Scaup, while *M. balthica* was a minor food despite being common in the area (Takekawa et al., unpubl. data).

Anthropogenic changes have strongly affected the prey communities of benthic feeders in San Francisco Bay. The fauna of San Pablo Bay consists mostly of introduced species (Cohen and Carlton 1998). *Potamocorbula amurensis* invaded in 1986 and quickly achieved numerical dominance in some parts of the bay (Carlton et al. 1990). This clam's euryhaline nature allows it to persist during high freshwater inflows when some other estuarine invertebrates retreat from the northern reach of San Francisco Bay (Nichols et al. 1990). While scaup readily feed on *P. amurensis*, its meat:shell ratio (dry mass) is about 66% that of *M. balthica* (0.065 vs. 0.099
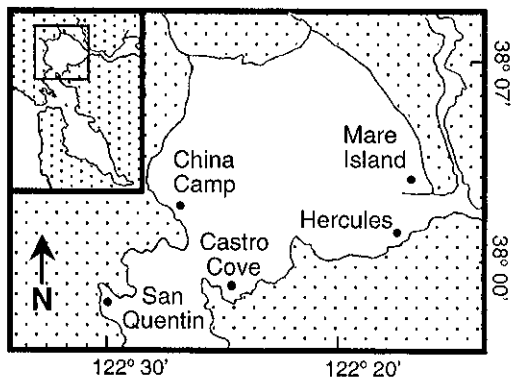

FIGURE 1.   San Pablo Bay in northern San Francisco Bay, California (inset), showing the five sites where we sampled clam density and scaup behavior.

for 6–24 mm shell lengths, Richman and Lovvorn, unpubl. data). In some cases, *P. amurensis* has been found to accumulate more contaminants than *M. balthica* (Brown and Luoma 1995).

To determine effects of prey availability and quality on wintering scaup, a link must be established between scaup feeding behavior and benthic community characteristics (Lovvorn and Gillingham 1996). The goal of this study was to describe the time-activity budgets of scaup at different sites in San Pablo Bay, and to evaluate effects of prey densities on scaup feeding behavior. Diving ducks often use different areas for feeding and resting (Nilsson 1969, 1972, Michot et al. 1994). If scaup congregate at certain sites to feed because of prey availability, then observing scaup might be less expensive than benthic sampling for inferring trends in prey availability and identifying important areas of prey concentrations.

METHODS

STUDY AREA

San Pablo Bay is in northern San Francisco Bay, California (Fig. 1). San Pablo Bay has a surface area of 215 km², roughly two-thirds of which is <2 m deep. Salinity fluctuates dramatically throughout the year with varying freshwater inflow: salinity at the upstream end of San Pablo Bay can vary from 2‰ during spring runoff to 23‰ during low inflows in late summer (Nichols 1979, Conomos et al. 1985). Sediments of the bay are mostly clay, silt, and some sand (Conomos et al. 1985), and the water in this shal-

low, windy area is very turbid. Five sites around San Pablo Bay, including one site in nearby San Quentin Bay (Fig. 1), were chosen for study based on their use by radio-marked scaup during winter 1998–1999 (Takekawa et al., unpubl. data) and their accessibility for sampling both behavior and benthos. Maximum tidal range at these sites was about 2.4 m, and scaup fed in subtidal areas as well as intertidal areas when flooded.

OBSERVATIONS OF BEHAVIOR

Scaup behavior was observed at the five sites (Fig. 1) from 12 January to 3 March 2000. Observations were not made earlier in fall or later in spring because both behavior observations and benthic sampling (see below) were very time intensive and could not be done at the same time. We started benthic sampling later than planned because of equipment problems, and did not have time or personnel to begin observations until benthic sampling was completed at the end of December. In spring, observations were stopped and benthic sampling started when scaup began leaving for spring migration.

Observation locations and times were assigned randomly to one of two observers. To ensure equal coverage of all daylight hours, daylight was divided into three equal periods, and 2-hr sessions within each period were randomly chosen for each observation day for each person. If scaup were not present at the assigned site and time, the observer went to the next assigned site. Focal-individual sampling (Altmann 1974) was used because other methods such as scan sampling would underestimate the number of feeding birds when many were underwater. We did not attempt to distinguish Lesser and Greater Scaup in the field because of their similar appearance. Male and female scaup were sampled in alternate sequence and observed continuously for 5 min through a 15–60× spotting scope or 80× Questar telescope. Scaup were randomly sampled by swinging the scope across the range of visible birds and selecting the individual closest to the center of the field of view where the scope came to rest (Lovvorn 1989). Unmarked individuals could usually be followed continuously during feeding bouts because they fed in loose flocks with little chance of confusing the focal individual with other birds. The activity of the focal individual was dictated into a tape recorder at 20-sec intervals (indicated by a met-

ronome) throughout the 5-min period. The beginning and end of all dives were recorded. The audio tapes were later transcribed, and dive duration was measured with a digital timer.

Scaup activities were classified into seven categories: feeding, dabbling, swimming, resting, sleeping, comfort movements, and other. We defined feeding to be diving or pausing between dives during a feeding bout (Byrkjedal 1997). Dabbling occurred when scaup were in very shallow water and could feed without diving. Swimming was movement across the surface of the water. Resting was inactivity with head up, whereas sleeping was inactivity with head tucked under the wing. Comfort movements included preening, bathing, shaking, and drinking. Other activities recorded were social interactions, alert postures, and flying.

Observers recorded ambient temperature and wind speed class (calm, <5 km hr^{-1}; breezy, 5–19 km hr^{-1}; windy, >20 km hr^{-1}) at the time of observations. Because water depth has been shown to affect diving duck feeding (Mitchell 1992), tide level in feet above mean lower low water was determined for each hour of observations according to a tide book (Tidelog 1999). Height and time of tides were adjusted for location within San Francisco Bay according to the tide book to correct for tidal lag along the estuarine gradient.

BENTHIC SAMPLING

The benthos was sampled at the five sites where scaup behavior was observed. Single transects at each site were established where the water was 0.3–3 m deep at mean lower low water. Transects were perpendicular to shoreline and 360 to 1400 m long, depending on the width of the area spanning these depths. Triplicate samples were taken at each of 10–15 stations spaced equidistantly along each transect. Samples were taken to a depth of 20 cm below the sediment surface with a stainless steel corer 10 cm in diameter; these cores were divided into layers of top 5 cm, middle 5 cm, and bottom 10 cm. Transects were sampled from 19 October to 17 December 1999 (fall period) and from 6 March to 19 April 2000 (spring period) after scaup departed for spring migration. The order in which different sites were sampled was the same in fall and spring. During the fall period, additional triplicate samples were taken at 1-m increments to a distance of 5 m downwind from each sta-

tion. These additional samples were taken for a concurrent study of invertebrate dispersion. While more samples were collected in the fall, the same stations on each transect were used and sampling effort was proportionately the same at each site in fall and spring.

Core samples were stored in plastic zipper-lock bags and were processed after collection or were frozen and later thawed for processing. All clams retained by a 1-mm sieve were identified to species and their shell length measured to the nearest 0.5 mm. Invertebrate densities were averaged over the triplicate samples at each sampling location.

STATISTICAL ANALYSES

Behavior data were tested for normality and equality of variance, and rank-transformed where appropriate. Percent time spent feeding was grouped by the hour to correct for possible dependence among samples taken at the same place and time. Percent time spent feeding was arcsine transformed before being used in least-squares multiple regression against various characteristics of prey (density and shell size of *P. amurensis* and *M. balthica*) and habitat (ambient temperature, time of day, wind speed, and tide height). Two-group *t*-tests were used to compare feeding and diving behavior between sex and season. Observational data were split into an early period (12 January to 5 February 2000) and a late period (7 February to 3 March 2000) for comparison with fall and spring benthic samples, assuming that scaup behavior when benthic samples were collected was similar to behavior during observations. Important predictor variables were selected with the best-subsets model selection procedure, where all possible combinations of variables are considered and the best model is chosen based on the adjusted R^2 value and number of variables (PROC REG, SAS Institute 1987).

Clam densities were compared between fall and spring by nested ANOVA and Bonferroni *t*-tests (PROC GLM, SAS Institute 1987). Differences in clamshell lengths among sites were tested by Bonferroni pairwise comparisons. Results were considered significant when $P < 0.05$. Results are presented as means $\pm$ SE except where otherwise noted.
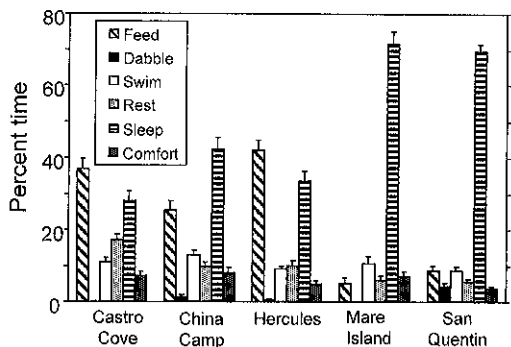

FIGURE 2. Mean $\pm$ SE percent time spent by scaup in different activities during daylight at five sites in San Pablo Bay, California, 12 January–3 March 2000 ($n = 1253$ focal individuals on 38 days). Sample sizes and tests among behaviors and sites are in Table 1.

RESULTS

SCAUP BEHAVIOR

Diurnal time-activity budgets of scaup varied between sites (MANOVA, Wilks' $\lambda = 0.76$, $F_{24,4338} = 15.19$, $P < 0.001$; degrees of freedom explained in Tabachnik and Fidell 2001). Scaup at the Mare Island and San Quentin sites mostly slept (69–72%), while both feeding (26–42%) and sleeping (28–42%) were common at the Castro Cove, Hercules, and China Camp sites (Fig. 2). Proportion of time spent swimming, resting, and performing comfort movements such as preening and bathing were similar at all sites, and generally were much less frequent than the dominant activities of sleeping or feeding (Table 1). Feeding by dabbling instead of diving occurred at low tides when water was very shallow over the mudflats. Other activities such as social interactions, being alert, and flying were rarely recorded and were not analyzed (aggressive interactions were almost never observed). Percent time spent feeding did not differ between the first half of the observation period (12 January–5 February) and the second half of the observation period (7 February–3 March; $t_{1262} = 1.3$, $P = 0.2$). Mean dive duration was shorter during the first half of the observation period (21.6 $\pm$ 0.4 sec for $n = 224$ individuals making 1468 dives) than during the second half of the observation period (24.7 $\pm$ 0.5 sec for $n = 195$ individuals making 1201 dives; $t_{417} = -4.8$, $P < 0.001$) regardless of tide level. Males and females did not differ in mean dive duration ($t_{417} = 1.1$, $P = 0.26$), but females spent

TABLE 1.   Mean ± SD percent time spent in different activities by scaup during daylight at five sites around San Pablo Bay (Fig. 1) from 12 January–3 March 2000. Means in rows followed by the same capital letter, and means in columns followed by the same lowercase letter, are not significantly different (Bonferroni multiple comparisons on rank-transformed data, experimentwise α = 0.05 for all tests combined).

	Castro Cove	China Camp	Hercules	Mare Island	San Quentin
n^a	244	233	274	132	370
Feed	36.9 ± 41.3 A,a	25.5 ± 38.1 C,a	42.2 ± 43.4 A,a	5.1 ± 19.3 B,ac	8.7 ± 24.2 B,ac
Dabble	0.1 ± 1.6 A,d	1.4 ± 10.0 AB,d	0.4 ± 4.0 A,f	<0.1 ± 0.5 A,a	4.3 ± 19.1 B,ef
Swim	11.0 ± 20.2 A,b	21.8 ± 22.3 A,a	9.0 ± 14.2 A,b	10.5 ± 22.8 AB,b	8.6 ± 18.9 B,b
Rest	17.0 ± 27.8 B,b	9.7 ± 20.6 AB,a	10.0 ± 22.4 A,c	5.8 ± 16.2 A,bc	5.5 ± 14.3 A,bc
Sleep	27.9 ± 42.5 B,b	42.4 ± 46.5 A,b	33.6 ± 43.7 AB,bd	71.6 ± 40.3 C,d	69.4 ± 42.2 C,d
Comfort	7.1 ± 19.7 A,c	8.0 ± 21.8 A,c	4.9 ± 14.5 A,ce	6.9 ± 18.7 A,bc	3.6 ± 12.0 A,ae

[a] Number of 5-min focal-individual samples.

more time feeding (27.7 ± 1.5%, n = 671) than males (20.0 ± 1.5%, n = 576; t_{1256} = 3.5, P < 0.001).

CLAM DENSITIES AND EFFECTS ON SCAUP BEHAVIOR

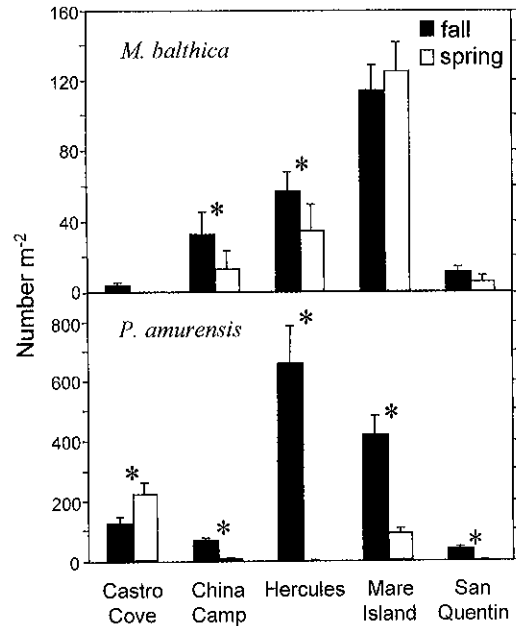*Potamocorbula amurensis* and *Macoma balthica* were the most abundant clams in benthic sam-

FIGURE 3.   Mean ± SE number of *Macoma balthica* and *Potamocorbula amurensis* clams m⁻² at five sites in San Pablo Bay, California, during the fall and spring sampling periods (19 October–17 December 1999, n = 514 samples with 3 cores per sample; and 6 March–19 April 2000, n = 68). Note different scales on ordinate axes. Bars marked with asterisks are significantly different (Bonferroni pairwise comparisons on ranked data, P < 0.05).

ples, although some *Mya arenaria* were also found. No *Gemma gemma* clams or *Ampelisca abdita* amphipods were encountered, although these introduced species have been common in other benthic studies in San Francisco Bay (Nichols and Thompson 1985a, Nichols and Pamatmat 1988). Densities (number m⁻²) of *M. balthica* and *P. amurensis* varied widely among sites, but *P. amurensis* was far more numerous than *M. balthica* in the fall and generally less numerous than *M. balthica* in the spring (Fig. 3). Densities of *P. amurensis* declined dramatically from fall to spring at all sites except Castro Cove, where they increased. *M. balthica* declines were less dramatic, and nonsignificant at 3 of 5 sites. Mean shell length of *P. amurensis* was smaller (8.0 ± 0.3 mm) than for *M. balthica* (16.5 ± 0.5 mm; Fig. 4). Almost all (97%) *P. amurensis* occurred in the top 5 cm of cores, with <2% each at 5–10 and 10–20 cm depth in the sediments. In contrast, only 48% of *M. balthica* were in the top 5 cm, with numbers declining gradually to 34% at 5–10 cm and 18% at 10–20 cm. Shell length of *M. balthica* was higher in deeper sediments (r^2 = 0.40, P < 0.001).

We tested for effects on percent time spent feeding of various factors: hours since sunrise, tide height, ambient temperature, wind speed, *P. amurensis* density, and *M. balthica* density. Shell lengths of *P. amurensis* and *M. balthica* were considered in the regression for the first period, but were not considered for the second period when these species were not detected at all sites (Fig. 3) and too few data were available on shell length. During the first half of the observation period, percent time feeding increased with increasing density of *P. amurensis* (partial R^2 = 0.15) but decreased with increasing density
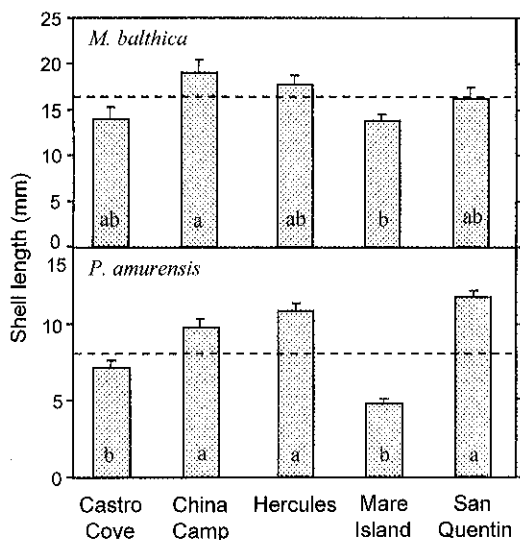
FIGURE 4. Mean ± SE shell length (mm) of the clams *Macoma balthica* (n = 135 stations containing clams) and *Potamocorbula amurensis* (n = 144) at five sites in San Pablo Bay, California, October 1999–April 2000. Note different scales on ordinate axes. For each species, bars with the same letters are not significantly different (experimentwise α = 0.05). Dashed lines show the grand mean for each species.

of *M. balthica* (partial R^2 = −0.19; Table 2). Hours since sunrise, tide height, and shell lengths of *M. balthica* and *P. amurensis* had significant but only slight effects. During the second half of the observation period, percent time spent feeding was still positively related to *P. amurensis* density and negatively related to *M. balthica* density, but these correlations were much weaker.

DISCUSSION

During daylight in San Pablo Bay, scaup at two sites mainly slept, whereas at the three other sites they mainly slept and fed. Females spent more time feeding than males, perhaps because of their smaller body size (Goudie and Ankney 1986). During fall migration, female Lesser Scaup on the upper Mississippi River also spent more time feeding (20%) compared to males (14%; Takekawa 1987). We do not know how much individual scaup might have used different sites for different activities (e.g., certain sites only for sleeping, and others for both sleeping and feeding). However, in a concurrent study, radio-marked individuals were often relocated at the same site for several days or even weeks,

and did not seem to have daily schedules of movement between sites (Takekawa et al., unpubl. data).

At some sites, scaup regularly fed during the day, instead of feeding mostly at night to avoid disturbance as reported in some other studies (Nilsson 1970, Pedroli 1982). Small watercraft did not pass by often, but when they did all waterfowl flushed from the site; large ferryboats and freighters were restricted to deep channels where scaup were not observed feeding or resting. On hunting days few scaup were seen near offshore hunting blinds, and scaup were sometimes absent from our observation sites when hunters were present. No observations were made before sunrise or after sunset because scaup were not close enough to shore to be seen with night-vision equipment. Thus, we could not compare daytime with nighttime activity (cf., Nilsson 1970, Bergan et al. 1989, Custer et al. 1996). However, concurrent radio-telemetry data indicated that scaup did not move to different sites from those they occupied during the day, and that scaup made only about 6% more dives at night than during crepuscular and daylight hours (Takekawa et al., unpubl. data).

In San Pablo Bay, tide height had little effect on time spent feeding by scaup, but the trend resembled that observed for Redheads (*Aythya americana*) in Louisiana, which fed more at low tides (Michot et al. 1994). In shallow water at very low tides, scaup would tip up or just submerge their heads to feed instead of diving, although they never walked out of the water to feed on exposed mudflats.

During the first half of the observation period, percent time spent feeding was clearly higher where densities of *P. amurensis* were higher (Table 2), and dive duration increased by 14% between early and late observations as the density of *P. amurensis* declined. The importance of this clam as food for scaup probably results from its relatively small size, high absolute and relative abundance, and occurrence near the sediment surface where it is readily accessible. Scaup tended to feed more where *P. amurensis* were smaller (Table 2). The similar Tufted Duck (*Aythya fuligula*) feeding on zebra mussels (*Dreissena polymorpha*) in the laboratory preferred smaller mussels because they were more easily handled and swallowed (Draulans 1982). When feeding in turbid waters (as in San Pablo Bay), Tufted Ducks selected smaller mussels

TABLE 2. Coefficients of partial determination (partial R^2) between percent time spent feeding by scaup during daylight and different variables in San Pablo Bay. Percentages of time feeding were respective means for early and late periods. Clam densities were the means (number m^{-2}) for five different sites during fall and spring periods of benthic sampling (Fig. 3). The early observation period had $n = 124$ hr including 651 5-min focal-individual samples collected on 16 different days, and the late period had $n = 119$ hr including 602 focal-individual samples on 22 days. Shell lengths were not included in the regression for the late period.

Variable	Partial R^2	P
Early period (12 January–5 February 2000)		
Potamocorbula amurensis density	0.15	<0.001
Macoma balthica density	−0.19	<0.001
Hours since sunrise	−0.03	0.02
Tide height above mean lower low water	−0.02	0.07
M. balthica shell length	0.01	0.13
P. amurensis shell length	−0.04	0.01
Late period (7 February–3 March 2000)		
P. amurensis density	0.05	0.01
M. balthica density	0.04	0.03

presumably to reduce the risk of taking mussels that were too large to swallow safely (Draulans 1982).

During the first half of our observation period, when *P. amurensis* was more abundant, scaup tended to feed less where *M. balthica* densities were higher (Table 2). *Macoma balthica* is larger, burrows deeper, and is probably more difficult to find, handle, and swallow than *P. amurensis*. Thus, although *M. balthica* can be an important food of both Greater and Lesser Scaup (Madsen 1954, Yocom and Keller 1961, Stewart 1962, Nilsson 1972, Perry and Uhler 1982), smaller clam species appear to be favored when they co-occur abundantly with *M. balthica* (Stewart 1962, Perry and Uhler 1982). Of birds containing food that were collected in San Pablo Bay during the winters of 1998–99 and 1999–2000, only 1 of 11 Lesser Scaup and 1 of 14 Greater Scaup contained *M. balthica*, whereas *P. amurensis* was the most important food of both species (Takekawa et al., unpubl. data). On the Atlantic and Gulf Coasts of North America, the clam *Mulinia lateralis* is often the major food of both scaup species (Cronan 1957, Harmon 1962, Stewart 1962, Perry and Uhler 1982). Like *P. amurensis*, this clam is small and lives at the sediment surface.

The San Quentin site may have been a resting area because the benthic community there was composed mostly of the clam *Mya arenaria* which scaup do not eat in San Francisco Bay, and the site was near an urban area so hunting did not occur there. Dominance of sleeping at

the Mare Island site is harder to explain because the benthic community there was composed of high densities of *P. amurensis*, and the area was exposed to hunting. Scaup might have fed more at the Mare Island site and depleted prey before observations began in January 2000. However, prey densities were higher there in early December 1999 than at other sites where feeding was more frequent. The observation point at Mare Island was at low elevation and observers did not have as wide a view of that area as at the other sites, so scaup feeding may have been relatively under-reported at this site.

Scaup preference for *P. amurensis* might have influenced the decrease in *P. amurensis* density at most sites between fall and early spring, while *M. balthica* density showed no consistent change (Fig. 3). It is unlikely that these relative trends between species resulted from increased freshwater inflow that occurs in this interval, because *P. amurensis* tolerates lower salinity than *M. balthica* (Castagna and Chanley 1973, Nicolini and Penry 2000). Predation can be important in controlling benthic populations (Posey et al. 1995), and diving ducks including scaup reduced densities of the clam *Corbicula fluminea* in a South Carolina pond over winter (Smith et al. 1986). In Lake Erie, diving ducks including scaup reduced zebra mussel densities in the short term; however, predation was not considered the main control of mussel populations, as habitat and density-dependent effects were also important (Hamilton and Ankney 1994). Recruitment from adjacent mussel beds maintained

mussel biomass from year to year (Hamilton et al. 1994).

Low correlations between densities of the preferred prey, *P. amurensis*, and percent time feeding (partial R^2 of 0.05 and 0.15; Table 2) might have resulted from the large area available to scaup in the San Francisco Bay system. Shallow water is an important habitat factor for various diving ducks including scaup (Jones and Drobney 1986, Mitchell 1992); thus, along with nearby rivers, sloughs, and salt ponds, this large shallow system appears to provide scaup with a wide range of potential feeding habitat. When prey densities at a given site are low, scaup may leave that site rather than forage at unprofitably low densities (Hamilton et al. 1994, Lovvorn and Gillingham 1996). Radio-telemetry indicated that many scaup moved upstream in the estuary from San Pablo Bay to Suisun Bay in January 2000 (Takekawa et al., unpubl. data). At that time, California received heavy rainfall after a dry autumn resulting in a rapid increase in freshwater inflow to San Pablo Bay. The sudden drop in salinity might have killed many clams in the Bay (Castagna and Chanley 1973), and inflowing sediments or shifting of sediments by winds might have buried or scoured clams (Kranz 1974, Ratcliffe et al. 1981, Nichols and Thompson 1985b). In such cases, scaup might find higher densities of an alternative clam food, *Corbicula fluminea*, upstream from San Pablo Bay, and might move there from less suitable feeding areas in San Pablo Bay. Greater Scaup in England switched feeding sites and prey species depending on prey availability (Quinn et al. 1996), and diving duck distributions responded to rising and falling zebra mussel populations in the Great Lakes (Hamilton and Ankney 1994). Other researchers have found weak correlations between the distributions of diving ducks and prey densities at large scales (Nilsson 1972, DeGraer et al. 1999).

Scaup feeding behavior would also correlate poorly with clam densities if densities were beyond the asymptote of the type II functional response of intake rate versus prey density (Lovvorn and Gillingham 1996). At densities beyond this asymptote, intake rate is limited by handling time and so cannot increase with increasing prey abundance. However, *P. amurensis* densities in San Pablo Bay during winter 1999–2000 were much lower than reported in past studies (Carlton et al. 1990, Nichols et al. 1990), and laboratory tests suggest that Lesser Scaup can increase intake of small clams near the sediment surface at densities up to at least 4000 m^{-2} (Richman and Lovvorn, unpubl. data). In our study, densities of *P. amurensis* caught in a 1-mm sieve did not exceed 1273 m^{-2} averaged over any triplicate subsample (maximum of 2207 m^{-2} among 1746 cores), so intake rates of scaup in San Pablo Bay were probably not limited by handling time but rather by search time as determined by prey density and dispersion.

Benthic communities in the San Francisco Bay system vary greatly with annual and seasonal fluctuations in freshwater inflow. Scaup wintering there might be flexible in where they feed because prey populations in different areas might not be similar from year to year. This variability makes it hard to identify specific areas of management concern. Our results suggest that monitoring scaup behavior is not an effective proxy for regular benthic sampling to infer prey conditions or identify key prey concentrations. Locally decimated clams probably rely on nearby populations for recolonization by young clams transported in the water column or along the bottom (Ratcliffe et al. 1981, Emerson and Grant 1991, Cummings et al. 1995). Thus, benthic feeders in San Pablo Bay probably depend on the existence of multiple local populations of benthic prey to buffer stochastic disturbances.

ACKNOWLEDGMENTS

LITERATURE CITED

ACCURSO, L. M. 1992. Distribution and abundance of wintering waterfowl on San Francisco Bay 1988–1990. M.Sc. thesis, Humboldt State University, Arcata, CA.

ALTMANN, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–267.

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.

BERGAN, J. F., L. M. SMITH, AND J. J. MAYER. 1989. Time-activity budgets of diving ducks wintering in South Carolina. Journal of Wildlife Management 53:769–776.

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.

BYRKJEDAL, I. 1997. Identifying inter-dive intervals in time-activity budget studies of diving ducks. Wildlife Biology 3:45–51.

CARLTON, J. T., J. K. THOMPSON, L. E. SCHEMEL, AND F. H. 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.

CASTAGNA, M., AND P. CHANLEY. 1973. Salinity tolerance of some marine bivalves from inshore and estuarine environments in Virginia waters on the western mid-Atlantic coast. Malacologia 12:47–96.

COHEN, A. N., AND J. T. CARLTON. 1998. Accelerating invasion rate in a highly invaded estuary. Science 279:555–557.

CONOMOS, T. J., R. E. SMITH, AND J. W. GARTNER. 1985. Environmental setting of San Francisco Bay. Hydrobiologia 129:1–12.

CRONAN, J. M. 1957. Food and feeding habits of the scaups in Connecticut waters. Auk 74:459–468.

CUMMINGS, V. J., R. D. PRIDMORE, S. F. THRUSH, AND J. E. HEWITT. 1995. Post-settlement movement by intertidal benthic macroinvertebrates: do common New Zealand species drift in the water column? New Zealand Journal of Marine and Freshwater Research 29:59–67.

CUSTER, C. M., T. W. CUSTER, AND D. W. SPARKS. 1996. Radio telemetry documents 24-hour feeding activity of wintering Lesser Scaup. Wilson Bulletin 108:556–566.

DEGRAER, S., M. VINCX, P. MEIRE, AND H. OFFRINGA. 1999. The macrozoobenthos of an important wintering area of the Common Scoter (*Melanitta nigra*). Journal of the Marine Biological Association of the United Kingdom 79:243–251.

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

EMERSON, C. W., AND J. GRANT. 1991. The control of soft-shell clam (*Mya arenaria*) recruitment on intertidal sandflats by bedload sediment transport. Limnology and Oceanography 36:1288–1300.

GOUDIE, R. I., AND C. D. ANKNEY. 1986. Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. Ecology 67:1475–1482.

HAMILTON, D. J., AND C. D. ANKNEY. 1994. Consumption of zebra mussels *Dreissena polymorpha* by diving ducks in Lakes Erie and St. Clair. Wildfowl 45:159–166.

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.

HARMON, B. G. 1962. Mollusks as food of Lesser Scaup along the Louisiana coast. Transactions of the North American Wildlife and Natural Resources Conference 27:132–138.

JONES, J. J., AND R. D. DROBNEY. 1986. Winter feeding ecology of scaup and Common Goldeneye in Michigan. Journal of Wildlife Management 50: 446–452.

KRANZ, P. M. 1974. The anastrophic burial of bivalves and its paleoecological significance. Journal of Geology 82:237–265.

LOVVORN, J. R. 1989. Food defendability and antipredator tactics: implications for dominance and pairing in Canvasbacks. Condor 91:826–836.

LOVVORN, J. R., AND M. P. GILLINGHAM. 1996. Food dispersion and foraging energetics: a mechanistic synthesis for field studies of avian benthivores. Ecology 77:435–451.

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

MICHOT, T. C., E. B. MOSER, AND W. NORLING. 1994. Effects of weather and tides on feeding and flock positions of wintering Redheads in the Chandeleur Sound, Louisiana. Hydrobiologia 279/280:263–278.

MITCHELL, C. A. 1992. Water depth predicts Redhead distribution in the lower Laguna Madre, Texas. Wildlife Society Bulletin 20:420–424.

NICHOLS, F. H. 1979. Natural and anthropogenic influences on benthic community structure in San Francisco Bay, p. 409–426. *In* T. J. Conomos [ED.], San Francisco Bay: the urbanized estuary. American Association for the Advancement of Science, Pacific Division, San Francisco, CA.

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(7.19).

NICHOLS, F. H., AND J. K. THOMPSON. 1985a. Persistence of an introduced mudflat community in south San Francisco Bay, California. Marine Ecology Progress Series 24:83–97.

NICHOLS, F. H., AND J. K. THOMPSON. 1985b. 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.

NICOLINI, M. H., AND D. L. PENRY. 2000. Spawning, fertilization, and larval development of *Potamocorbula amurensis* (Mollusca: Bivalvia) from San Francisco Bay, California. Pacific Science 54: 377–388.

NILSSON, L. 1969. Food consumption of diving ducks wintering at the coast of south Sweden in relation to food resources. Oikos 20:128–135.

NILSSON, L. 1970. Food-seeking activity of south Swedish diving ducks in the non-breeding season. Oikos 21:145–154.

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.

NYSEWANDER, D. R., AND J. R. EVENSON. 1998. Status and trends for selected diving duck species examined by the Marine Bird Component, Puget Sound Ambient Monitoring Program, Washington Department of Fish and Wildlife. Proceedings of the Puget Sound Research Conference 1998, 2: 847–867. Puget Sound Water Quality Action Team, Olympia, WA.

PEDROLI, J. C. 1982. Activity and time budget of Tufted Ducks on Swiss lakes during winter. Wildfowl 33:105–112.

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.

POSEY, M., C. POWELL, L. CAHOON, AND D. LINDQUIST. 1995. Top down vs. bottom up control of benthic community composition on an intertidal tideflat. Journal of Experimental Marine Biology and Ecology 185:19–31.

QUINN, J. L., L. STILL, M. C. CARRIER, J. S. KIRBY, AND P. LAMBDON. 1996. Scaup *Aythya marila* numbers and the cockle *Cardium edule* fishery in the Solway Firth: are they related? Wildfowl 47: 186–193.

RATCLIFFE, P. J., N. V. JONES, AND N. J. WALTERS. 1981. The survival of *Macoma balthica* (L.) in mobile sediments, p. 91–108. *In* N. V. Jones and W. J. Wolff [EDS.], Feeding and survival strategies of estuarine organisms. Plenum Press, New York.

SAS INSTITUTE. 1987. SAS/STAT guide for personal computers. SAS Insitute, Cary, NC.

SMITH, L. M., L. D. VANGILDER, R. T. HOPPE, S. J. MORREALE, AND I. L. BRISBIN. 1986. Effect of diving ducks on benthic food resources during winter in South Carolina, U.S.A. Wildfowl 37:136–141.

STEWART, R. E. 1962. Waterfowl populations in the upper Chesapeake region. U.S. Fish and Wildlife Service Special Scientific Report—Wildlife 65, Washington, DC.

TABACHNIK, B. G., AND L. S. FIDELL. 2001. Using multivariate statistics. 4th ed. Allyn & Bacon, Boston.

TAKEKAWA, J. Y. 1987. Energetics of Canvasbacks staging on an Upper Mississippi River pool during fall migration. Ph.D. dissertation, Iowa State University, Ames, IA.

TIDELOG. 1999. Daily tide graphics based on predictions by the National Ocean Service. Pacific Publishers, Bolinas, CA.

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.