

# Niche overlap, threshold food densities, and limits to prey depletion for a diving duck assemblage in an estuarine bay

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**ABSTRACT:** Planning for marine conservation often requires estimates of the amount of habitat needed to support assemblages of interacting species. During winter in subtidal San Pablo Bay, California, the 3 main diving duck species are lesser scaup *Aythya affinis* (LESC), greater scaup *A. marila* (GRSC), and surf scoter *Melanitta perspicillata* (SUSC), which all feed almost entirely on the bivalve *Corbula amurensis*. Decreased body mass and fat, increased foraging effort, and major departures of these birds appeared to result from food limitation. Broad overlap in prey size, water depth, and location suggested that the 3 species responded similarly to availability of the same prey. However, an energetics model that accounts for differing body size, locomotor mode, and dive behavior indicated that each species will become limited at different stages of prey depletion in the order SUSC, then GRSC, then LESC. Depending on year, 35 to 66% of the energy in *Corbula* standing stocks was below estimated threshold densities for profitable foraging. Ectothermic predators, especially flounders and sturgeons, could reduce excess carrying capacity for different duck species by 4 to 10%. A substantial quantity of prey above profitability thresholds was not exploited before most ducks left San Pablo Bay. Such pre-depletion departure has been attributed in other taxa to foraging aggression. However, in these diving ducks that showed no overt aggression, this pattern may result from high costs of locating all adequate prey patches, resulting reliance on existing flocks to find food, and propensity to stay near dense flocks to avoid avian predation. For interacting species assemblages, modeling profitability thresholds can indicate the species most vulnerable to food declines. However, estimates of total habitat needed require better understanding of factors affecting the amount of prey above thresholds that is not depleted before the predators move elsewhere.

**KEY WORDS:** Carrying capacity · Foraging energetics models · San Francisco Bay benthos · San Pablo Bay · Surf scoter · Greater scaup · Lesser scaup · *Corbula amurensis*

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## INTRODUCTION

As marine habitats are degraded by human activities, it is often important to estimate the extent and quality of habitat needed to sustain animal popula-

tions that currently exist or might be restored. Such estimates typically focus on 'carrying capacity', which has been calculated for diverse marine taxa including crabs (Seitz et al. 2008), fish (Luo et al. 2001), sea otters *Enhydra lutris* (Laidre et al. 2002), and

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birds (Nolet et al. 2006). For single species, computer models to estimate carrying capacity, so far parameterized mainly for waterbirds, have been developed for general use (Stillman 2008, Stillman & Goss-Custard 2010).

However, for multiple species with similar diets, predicting effects of diminishing habitat requires knowing how shrinking resources might be partitioned to mediate coexistence and avoid competitive exclusion (Werner 1979, Zwarts & Wanink 1993, De Leeuw 1999, Friedlaender et al. 2011). In some cases, high relative abundance or value of a single prey species may lead generalist predators to compete indiscriminately for the same prey (van Eerden et al. 1997). In these situations, we expect partitioning of the same sizes of prey in space, e.g. by water depth and associated distance from shoreline. In the absence of spatial partitioning or behavioral interference (Persson 1985), the predators' relative persistence may depend on aspects such as body size that affect the prey density each species needs to forage profitably as prey becomes limiting (Richman & Lovvorn 2009). If so, one cannot target habitat conservation for a single species independently of others, but rather must maintain food stocks required to support profitable foraging by that species within a mix of competing predators.

The above issues apply to avian benthivores in San Francisco Bay. San Francisco Bay has long been a primary wintering area on the Pacific coast of North America for diving ducks. The most abundant diving duck species there have been lesser scaup *Aythya affinis* (LESC), greater scaup *A. marila* (GRSC), and surf scoter *Melanitta perspicillata* (SUSC). Although these species are found throughout the San Francisco Bay complex, highest densities have usually occurred in San Pablo Bay in the northern reach (Fig. 1; Accurso 1992). However, unvegetated salt ponds surrounding the bay are being restored to tidal salt marsh, eliminating substantial habitat for LE SC which feed both within diked ponds and in the bay outside the dikes. Breaching of dikes around salt ponds is also expected to alter the elevation, slope, and sediment quality of mud flats outside the dikes, as sediments move into formerly impounded areas with subsided soils. Moreover, there has been a gradual decrease in the extent of shoal areas in San Pablo Bay, mainly due to sediment retention by dams upstream. These changes are expected to decrease the extent and quality of foraging habitat for diving ducks in San Pablo Bay.

For at least the last half-century, the invertebrate prey community in San Pablo Bay has been strongly dominated by bivalves (Painter 1966, Thompson &

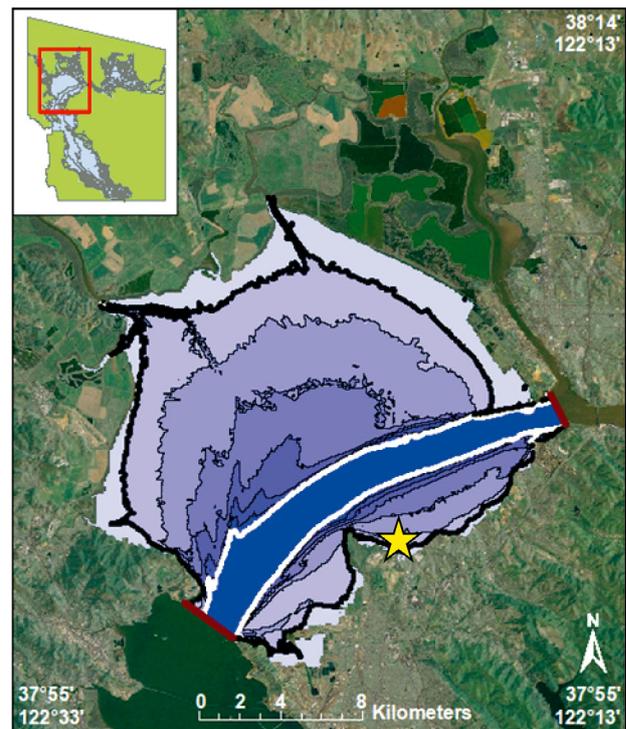


Fig. 1. San Pablo Bay within the San Francisco Bay estuary (inset), showing diked salt ponds of varying productivity, and bathymetric contours at 1 m intervals (shades of blue). The thick black line delineates the lower extent of intertidal depths ( $>0$  m MLLW, 50 km<sup>2</sup>), and the thick white line the lower extent of 'subtidal shoals' (0 to  $-6$  m MLLW, 208 km<sup>2</sup>). Maximum tidal range is about 2.4 m. ★: Capture site of radio-marked lesser and greater scaup. Bathymetry is from a US Geological Survey grid coverage based on 1983 NOAA/NOS surveys at 50 m resolution (<http://sfbay.wr.usgs.gov/sediment/sfbay/downloads.html>)

Nichols 1981, Peterson & Vayssières 2010). Of the 2 bivalve species now common (both exotic), *Corbula amurensis* (hereafter *Corbula*) is far more abundant than *Macoma petalum* and is a superior food (Richman & Lovvorn 2004). In winter 1999–2000, 4 of 5 sampling sites around San Pablo Bay showed major overwinter declines of suitably sized bivalve prey for diving ducks (Poulton et al. 2002, 2004). Perhaps as a result, diving duck numbers in San Pablo Bay, which are high from fall arrival through December, drop dramatically in January. In addition to bivalve declines over winter, bivalve numbers decreased over multiple years in the 2000s in at least some parts of San Francisco Bay. Direct environmental effects on recruitment or mortality of clams, and predation by several hundred thousand birds, may have played a role. Bivalve declines may also have resulted from climate-driven oceanic changes that increase the abundance or seasonal presence of fish and inverte-

brate predators in the bay (Cloern et al. 2007). These patterns suggest that in San Pablo Bay, food now becomes limiting to avian benthivores during winter, and limitation may become more severe under some climate scenarios. Decreased survival of either adult or juvenile bivalves may alter the size structure of prey, thereby favoring certain predator species over others (Richman & Lovvorn 2009).

Such interactions among birds are complicated by ectothermic predators whose diets can include the same prey, such as white sturgeon *Acipenser transmontanus*, starry flounder *Platichthys stellata*, and Dungeness crab *Cancer magister*. Smaller ages or species of ectothermic predator may affect the winter prey base mainly by consuming earlier life stages during spring and summer. However, the larger ectothermic predators can compete directly with ducks for the same sizes of prey.

In this paper, we develop an approach to estimating the habitat needed by an interacting species assemblage. First, we explore the degree of niche overlap among the 3 main avian benthivores in subtidal San Pablo Bay during winter. Given those results, we present a simulation model to calculate threshold prey densities required for profitable foraging by each duck species. We then use those thresholds to estimate the numbers of each species that the prey base could have supported during 3 winters for which benthic data are available. Although all these duck species will use intertidal areas when flooded, we restrict our analyses to subtidal elevations (0 to -6 m Mean Lower Low Water, MLLW; Fig. 1) and thus exclude intertidal areas which may be impacted by restoration of adjacent salt ponds. We also explore possible effects of ectothermic predators, which might reduce the prey base for diving ducks.

## MATERIALS AND METHODS

### Structure of energy balance model

The threshold prey density for profitable foraging is the density at which energy gain balances total cost (Fig. 2). Rates of energy gain depend on (1) prey energy content and digestibility, (2) ingestion rates (functional responses) for different prey densities and sizes, and (3) relative spatial coverage of those attributes based on field samples at stations throughout the area (Lovvorn & Gillingham 1996, Lovvorn et al. 2009). Energy costs include the immediate expense during foraging bouts, as well as prorated costs of all other activities when the birds are not foraging.

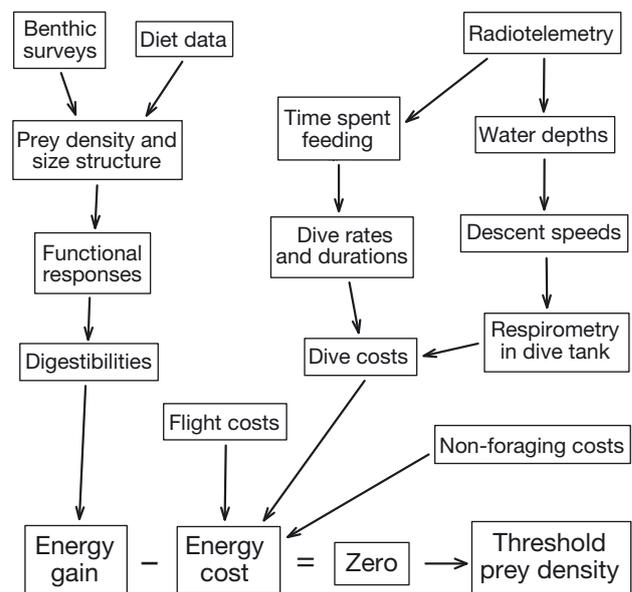


Fig. 2. Structure of the simulation model for estimating threshold densities of prey above which diving ducks can achieve positive energy balance

We did not use an individual-based model to simulate variations in search costs (cf. Lovvorn & Gillingham 1996, Stillman & Goss-Custard 2010). Costs of searching for adequate prey patches can affect profitability thresholds, and such costs can vary with prey dispersion. However, the resolution of our radiotelemetry data was inadequate to characterize individual searching movements by the 3 diving duck species at the scale of spatial variation of prey density throughout the bay. We did, however, include variations among species in costs of surface-swimming and diving at a local scale, as estimated from time-activity budgets in the field and cost measurements on captive ducks.

### Duck body mass and fat, diet, and prey size selection

To determine body mass, body fat, and diet, we collected diving ducks with shotguns in San Pablo Bay from October to mid-March 1998 to 2000 (LESC, GRSC) and 2004 to 2005 (SUSC). LESG and GRSC were collected from shorelines, whereas SUSC were collected offshore from a 4 m skiff. Collecting methods, diet and carcass analyses, and processing of benthic samples taken near sites where individual ducks were collected are described in the supplement at [www.int-res.com/articles/suppl/m476p251\\_supp.pdf](http://www.int-res.com/articles/suppl/m476p251_supp.pdf).

### Radio-telemetry and aerial surveys

Both scaup species were captured with swim-in corral traps at a site along the south shoreline of San Pablo Bay (Fig. 1) from October to December 1998 and 1999. Scoters were captured from small boats with a net gun (Coda Enterprises) from November to December 2003 and 2004. Transmitters, procedures for implanting transmitters, bird release protocols, accuracy of radio-locations, and schedules for obtaining radio-locations are described in the supplement.

Our telemetry surveys covered the entire San Pablo Bay each day. Based on diurnal, crepuscular, and nocturnal locations, there was no evidence that space use varied in consistent diel patterns. Instead, an individual bird typically remained in the same general location for several days or weeks, and its movements within that area were mostly aligned with tidal schedules. Multiple data points were taken for each individual bird during each month of our study. For our space use analysis, we used 5 randomly selected points per bird per month to avoid unequal weighting of birds with higher numbers of monthly locations. Fixed-kernel home ranges that encompassed 50 and 95% of radio-locations were estimated with Hawth's Tools in the geographic information system ArcGIS 9.3 (ESRI). Overlap in space use among the 3 duck species was determined by the Volume of Intersection Index (Mills-paugh et al. 2004). We also determined the chronology of departure from San Pablo Bay of 58 LESC and 59 GRSC radio-marked in the bay during October 1998 and 1999, and of 53 SUSC radio-marked in November 2003 and 2004 (Fig. S1 in the supplement at [www.int-res.com/articles/suppl/m476p251\\_supp.pdf](http://www.int-res.com/articles/suppl/m476p251_supp.pdf)).

From 2 October to 21 February 1988–1989 and 1989–1990, aerial counts of ducks in San Pablo Bay were conducted every 2 weeks. In winter 2004–2005, 2005–2006, and 2006–2007, aerial counts were conducted in early December (30 November to 8 December), early February (1 to 6 February), and early March (1 to 8 March, first 2 winters only). LESC and GRSC cannot be distinguished in aerial surveys, but only by examining birds in the hand. Thus, ratios of LESC to GRSC in aerial counts were taken from scaup trapped along the south shoreline of San Pablo Bay from October to December (Fig. 1). For aerial counts in 1989–1990, during which exceptionally large numbers of scaup were present starting in mid-October when LESC predominate, we used the value of 74% LESC from scaup trapped in 1999. For aerial counts in 1988–1989, when total numbers of scaup were much lower, we used the value of 44% LESC among scaup captured in 1998. Rather than depend-

ing on exact numbers of each species in a given year, our model was intended to evaluate a wide range of possible conditions. Thus, these values were used to represent very high versus much lower populations of scaup, which appear to be driven largely by annual variations in numbers of LESC.

### Behavior, energy costs, and intake rates

Details of behavior observations and activity cost estimates are described in the supplement. Briefly, diving ducks were observed through a 6 to 130× telescope (Questar Corporation) around San Pablo Bay during daylight from October to March 1988–1989 and 1989–1990. Focal individuals were observed continuously for 3 min. For radio-marked birds, feeding was inferred from intermittent attenuation of telemetry signals at the time each bird was located (Lewis et al. 2005). Energy costs of activities at the water surface were based on respirometry of captive ducks. Energy costs of aerial flight were calculated with Flight for Windows 1.22 software ([www.bio.bristol.ac.uk/people/pennycuick.htm](http://www.bio.bristol.ac.uk/people/pennycuick.htm)).

Costs of diving were based on respirometry of captive ducks in tanks 2 m deep, at water temperatures similar to the mean for San Francisco Bay during winter. (The mean dive depth for radio-marked individuals of all 3 species in subtidal areas of San Pablo Bay was about 2 m; see 'Results'.) Time spent at the bottom during dives was based on descent and ascent rates observed in dive tanks, and dive durations observed in the field. Dive durations (mean  $\pm 1$  SD) observed in San Pablo Bay (18.3  $\pm$  5.8 s for scaup, 26.9  $\pm$  6.8 s for SUSC; see 'Results') were assumed to correspond to the mean dive depth of radio-marked individuals of about 2 m. Applying descent and ascent speeds for 2 m dives, and subtracting the resulting descent and ascent durations from dive durations observed in the field, we estimated mean bottom durations of 12.9 s for LESC, 13.3 s for GRSC, and 18.9 s for SUSC. In uncertainty analyses, varying these bottom durations had little effect on model predictions for a given species (see 'Results').

Functional responses (numbers of prey consumed per unit time foraging at the bottom at different prey densities) were based on experiments with captive diving ducks feeding on prey buried in trays of sand at the bottom of a tank 2 m deep (Richman & Lovvorn 2009). Ash-free dry mass (AFDM, g), energy content, and assimilation efficiency for *Corbula* of different shell lengths were calculated from equations in Richman & Lovvorn (2004).

### Benthic sampling

On 5 to 7 September 1990, 10 September 1993, and 27 to 29 September 1995, single samples were taken with a Ponar grab at 54 stations on a regular grid throughout San Pablo Bay (Fig. 3). This grab sampled about 0.053 m<sup>2</sup> of the bottom to a depth in the sediments of about 10 cm. All *Corbula* retained by a 0.6 mm sieve were counted and their shell lengths measured to the nearest 0.1 mm. These samples were collected and processed by the California Department of Water Resources. Recruitment and growth of *Corbula* over winter is minimal (Parchaso & Thompson 2002), so the standing stock present in September was assumed to be the stock initially available for the rest of winter.

### Estimation of potential duck use-days

For each diving duck species in each year that the entire grid was sampled (1990, 1993, 1995), functional responses for *Corbula* were calculated for the areal density and mean shell length at each of the 54 stations. With the energetics model for each duck species, we then iteratively determined combinations of water depth from 0 to 6 m, *Corbula* density from 100 to 40 000 m<sup>-2</sup>, and *Corbula* shell length from 1 to 15 mm for which profit (energy gain minus cost, including overhead costs when not feeding) was near zero. Water depth over this range had negligible effects on profit. For values yielding near-zero profit, we regressed *Corbula* density on shell length to obtain an equation for each duck species that predicted the threshold density of *Corbula* of a given mean shell length required for profitable foraging. Threshold densities were in the order SUSC > GRSC > LESC (see 'Results').

As we observed almost no aggressive interactions within or among the diving duck species, and there was broad overlap among species in prey size, water depth, and location (see 'Results'), we assumed that all 3 species would feed opportunistically in any patch with prey density higher than their respective profitability thresholds. Based on the mean shell length of *Corbula* at each station, we then calculated the total amount of energy available within each bin of clam density: above the threshold for SUSC, below the SUSC threshold but above that for GRSC, and below the GRSC threshold but above that for LESC. Total energy available within each density bin was then partitioned among the duck species that could feed profitably at the respective clam densities,

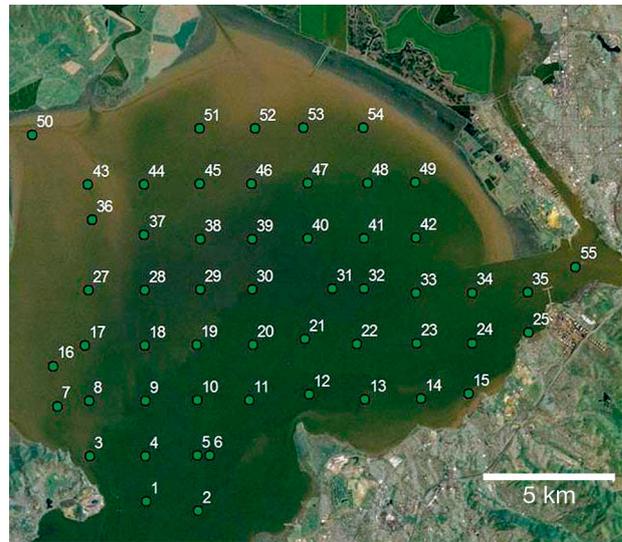


Fig. 3. Sampling stations for the clam *Corbula amurensis* in San Pablo Bay in September 1990, 1993, and 1995. Stns 1 through 55 (there was no Stn 26) were used in this analysis

according to relative numbers of those bird species weighted by their respective energy requirements.

Both the total energy in *Corbula* clams and the energy available to each duck species was extrapolated to the entire subtidal shoals of San Pablo Bay. To do that, we assumed that each station represented an area equal to the total area of the shoals (0 to -6 m MLLW, 208 km<sup>2</sup>) divided by 54 (the number of stations; Fig. 3). The energy available to each species was divided by that species' daily energy expenditure (DEE) to yield the total number of use-days of each species that the shoals could support starting in October. DEE (kJ d<sup>-1</sup> bird<sup>-1</sup>) estimated by the model was 811 for LESC, 1040 for GRSC, and 1094 for SUSC.

Aerial counts (see 'Radio-telemetry and aerial surveys' above) yielded daily mean numbers of each diving duck species over periods from October through January (123 d) and October through mid-April (197 d). These means were used to estimate the total number of use-days of each species that occurred during these periods, and the observed values were then compared to model estimates of total use-days available for each species starting in October.

The aerial counts were not in the same years as benthic sampling. However, the aerial surveys included winters with extremely high (1989–1990) and much lower (1988–1989) duck numbers, and benthic sampling included a year with very high densities of smaller *Corbula* (1993) as well as years with much lower densities of larger *Corbula* (1990, 1995) (see 'Results'). Our model was not intended to simulate

conditions for particular years in which all variables were measured simultaneously. Rather, our goal was to evaluate combinations of a range of possible conditions, as indicated by the variation in different variables among years when they were measured. Thus, our simulations included combinations of low and high numbers of ducks, and low and high numbers of *Corbula* of differing size structure.

### Consumption by ectothermic predators

Estimates of total prey biomass available to avian benthivores must also account for consumption by ectothermic predators. Recruitment and growth of *Corbula* over winter is minimal (Parchaso & Thompson 2002). Moreover, available data indicate that ectothermic predators, with their lower energy needs, can continue to forage profitably after prey densities have fallen to levels that no longer support the high intake rates needed by endothermic birds (Eggleston et al. 1992, Richman & Lovvorn 2009). Thus, estimated total consumption by the main ectothermic predators over a simulation period of October through January was subtracted from the standing stock of suitable prey measured in September to yield the number of ducks potentially displaced by ectotherms.

Predators present in appreciable numbers in late fall and winter that share prey with diving ducks include white sturgeon, starry flounder, and Dungeness crab (Kohlhorst et al. 1991, Orsi 1999). Methods and values used to estimate consumption by these ectothermic predators are in the supplement.

### Uncertainty analyses

We investigated effects of varying the values of selected parameters on model estimates of profit per dive using LESC and the prey base of *Corbula* in 1990. In most cases, we did not vary parameters by an arbitrary constant percentage, but rather over a range of values considered realistic for each parameter (Table 1). The rationale for ranges used for different variables is explained in the supplement. For uncertainty analyses, the value of each parameter for each of 300 iterations was randomly chosen from within the stated ranges, assuming a uniform distribution.

After simulations, the estimated variable (profit per dive) and all randomly chosen input parameters for each iteration were ranked across all iterations, and

Table 1. Parameters and their ranges used in uncertainty analyses of factors affecting profit per dive (energy gain minus cost, including daily overhead) of female lesser scaup for the mean *Corbula* density in 1990 of 1162 m<sup>-2</sup> and water depth of 2 m. For explanation of ranges, see the supplement at [www.int-res.com/articles/suppl/m476p251\\_supp.pdf](http://www.int-res.com/articles/suppl/m476p251_supp.pdf)

Parameter	Baseline	Range
Mean <i>Corbula</i> shell length (mm)	9.1	5.0–12.0
Functional response (prey s <sup>-1</sup> ) <sup>a</sup>	0.986	0.887–1.085
Time at the bottom per dive (s)	12.9	6.7–19.1
Feeding time per day (h)	5.12	3.50–8.88
Dive rate while feeding (dives min <sup>-1</sup> )	1.71	0.92–2.50
Disturbance flight time per day (min)	0	0–29

<sup>a</sup>Number of prey ingested per second at the bottom at a given prey density

we performed multiple regression of profit per dive against all parameter values. Relative partial sums of squares (RPSS) for ranked data indicated the proportion of variance in profit per dive explained by variation of individual parameters, with effects of the other parameters statistically removed (Lovvorn & Gillingham 1996 and references therein). We also report partial coefficients of determination (partial r<sup>2</sup>), because parameters can show high correlation but account for small residual variances as indicated by RPSS.

## RESULTS

### Duck body mass, fat content, behavior, and diet

For adult females in San Pablo Bay, the mean body mass of GRSC and S USC did not differ in either early or late winter (Fig. 4A; to simplify comparisons, we used only adult females for which we had higher and more consistent sample sizes). In early winter, the mass of GRSC was 34% higher, and that of S USC about 25% higher, than that of LESC. Samples of scaup yielded no LESC in late winter because they were scarce by that time in San Pablo Bay. Body mass declined by 18% in GRSC and 17% in S USC from early to late winter (late-winter samples were for birds that remained after most had left). All 3 species began winter with similar percent body fat, and GRSC and S USC had the same percent body fat in late winter (Fig. 4B). Thus, there was no indication that either GRSC or S USC had a more favorable energy balance than the other in San Pablo Bay over winter.

Based on daytime visual observations, scoters made fewer but longer dives than scaup, so that total percentage of time spent feeding was the same

over winter (17 to 18%; Table S1 in the supplement at [www.int-res.com/articles/suppl/m476p251\\_supp.pdf](http://www.int-res.com/articles/suppl/m476p251_supp.pdf)). Intermittent attenuation of radio signals showed that in both scaup species, total time spent feeding increased dramatically from November to February, especially at night (Fig. S2 in the supplement). SUSC also increased time spent feeding during the day from November to January, but decreased time feeding during the early part of the night when radio-locations were obtained.

In GRSC, the total dry mass of animal foods was 93% *Corbula* in 1998–1999 ( $n = 14$ ), and almost 100% of prey they obtained from subtidal habitats was *Corbula* in 1999–2000 ( $n = 13$ ). In both years, the diet of LESC was 99 to 100% *Corbula* ( $n = 13$  birds that con-

tained food in their esophagi). SUSC were collected in 2003–2004 and 2004–2005, when they ate almost entirely *Corbula* ( $n = 22$ ). Benthic sampling from 1999 through 2005 throughout the subtidal shoals showed that *Corbula* had overwhelming abundance and biomass. Thus, during most of the 1990s and 2000s, the ability of the subtidal shoals of San Pablo Bay (0 to –6 m MLLW) to sustain wintering populations of diving ducks depended almost entirely on *Corbula*. For modeling purposes, we restricted our analyses to this bivalve species.

### Overlap of prey size

There was almost 90% overlap of the ranges of *Corbula* shell lengths taken by LESC and GRSC (Fig. 5). The somewhat larger sizes eaten by LESC probably resulted from the difference in sampling dates: for birds that contained food, all LESC were collected in November to December, whereas all GRSC were collected in February to March when overall clam abundance was probably much lower. This difference in sampling dates resulted from seasonal asynchrony in use of San Pablo Bay by the 2 scaup species, which cannot be distinguished except in the hand and were collected opportunistically. The scoters were collected 4 to 5 yr later and much farther from shore, where grab samples indicated that the

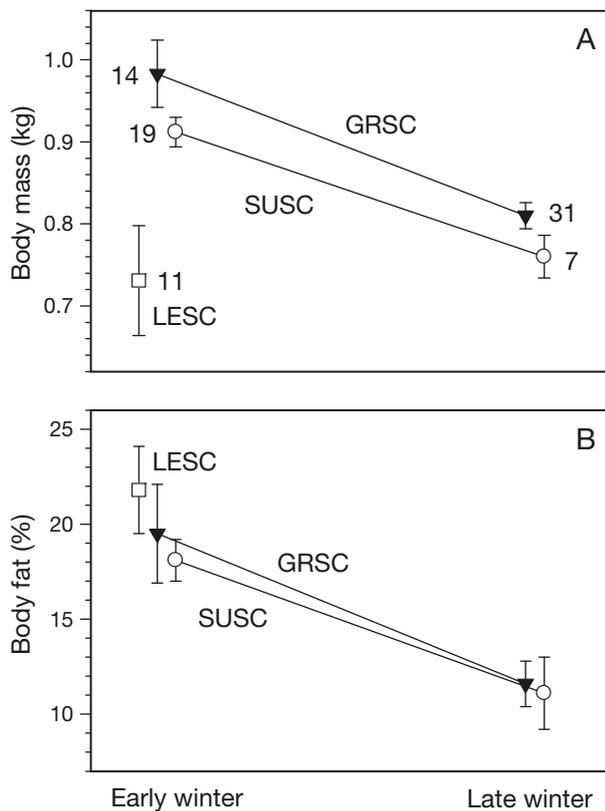


Fig. 4. *Aythya affinis*, *A. marila*, and *Melanitta perspicillata*. Mean  $\pm$  1 SE of (A) body mass and (B) percent body fat of adult female lesser scaup (LESC), greater scaup (GRSC), and surf scoters (SUSC) collected in San Pablo Bay during early winter (October through early January) and late winter (late January through early March) of 1998 to 2000 (scaup) and 2004 to 2005 (scoters). Sample sizes are in the upper panel. Body fat is expressed as percentage of ingesta-free fresh mass including plumage. Mean body masses of GRSC and SUSC did not differ ( $t$ -tests) in either early ( $p = 0.09$ ,  $df = 32$ ,  $F = 3.03$ ) or late winter ( $p = 0.17$ ,  $df = 37$ ,  $F = 2.00$ ), and there were no differences among species in percent fat in early (ANOVA,  $p = 0.41$ ,  $df = 43$ ,  $F = 0.91$ ) or late winter ( $t$ -test,  $p > 0.85$ ,  $df = 37$ ,  $F = 0.04$ )

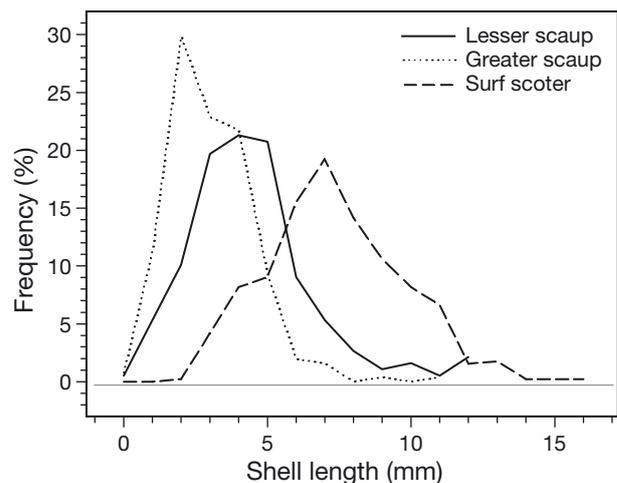


Fig. 5. *Corbula amurensis*. Shell lengths of the clam *C. amurensis* in esophagi of lesser scaup (LESC) and greater scaup (GRSC) collected in nearshore areas from 9 November to 3 December 1999 (LESC) and 17 February to 6 March 1999 and 2000 (GRSC), and in surf scoters collected in offshore areas from 29 October 2003 to 24 February 2004 and from 28 October to 23 November 2004 in San Pablo Bay. As an example, the tick on the x-axis for 2 mm represents shell lengths  $\geq 2$  and  $< 3$  mm

Table 2. *Aythya affinis*, *A. marila*, and *Melanitta perspicillata*. Percent numbers of the bivalves *Corbula amurensis* and *Musculista senhousia* of different shell lengths (6 mm bins) in esophagi of lesser scaup (LESC) and greater scaup (GRSC) in 1998 to 2000, and surf scoters (SUSC) in 2004 to 2005, collected in San Pablo Bay, compared to percent numbers in grab samples taken near sites where individual birds were collected. Sample sizes indicate either numbers of esophagi, or numbers of sampling stations for grabs, that contained these bivalves, with numbers of bivalves in parentheses. The p-value is for a chi-square test of equality of proportions in esophagi versus grabs

Duck species	Prey species	Esophagi				Grabs				p
		n	≤6	6–12	12–18	n	≤6	6–12	12–18	
LESC	<i>Corbula</i>	13 (188)	78	20	2	31 (310)	76	22	2	0.89
GRSC	<i>Corbula</i>	18 (258)	96	4		25 (194)	78	21	1	<0.01
	<i>Musculista</i>	3 (19)	5	53	42					
SUSC	<i>Corbula</i>	17 (452)	22	74	4	22 (718)	35	63	2	0.02

larger prey they consumed (Fig. 5) corresponded to larger prey available (Table 2). Despite these differences, the size range of *Corbula* eaten by SUSC included 83 and 81% of the ranges consumed by LESG and GRSC, respectively. Due to differing months, years, and locations of collections, our data do not allow tests for differences in prey sizes taken by the 3 duck species under the same conditions. However, these species all appear to find a wide range of prey sizes acceptable depending on availability.

Grab samples taken near locations where ducks were collected indicated that individual *Corbula* >12 mm long were uncommon during both periods of this study (Table 2). Sizes of *Corbula* eaten by LESG in early winter corresponded closely to sizes available, whereas GRSC in late winter contained smaller *Corbula* than were available in the immediate vicinity (cf. Fig. 5). However, consumption of many 12 to 18 mm *Musculista senhousia* by GRSC at 1 site (Point San Pablo) indicates that GRSC will readily eat clams >12 mm long if they are available. During early winter in San Pablo Bay, SUSC tended to contain larger *Corbula* than were available, but many small clams were eaten (Table 2).

In summary, it appears that GRSC and SUSC will readily eat the same size ranges of bivalves depending on availability. LESG consumption closely follows availability for clams <12 mm long, which comprised 98 to 99% of those present in San Pablo Bay during both periods (Table 2). If these duck species were feeding subtidally on the same prey base, their dietary flexibility and broad prey size overlap suggest they would similarly focus on the most available prey species and sizes (cf. Pöysä 1986). For initial model-

ing in the subtidal zone, we assumed that all 3 duck species eat *Corbula* >1 mm long in proportion to availability at a given site.

### Overlap of elevation and spatial use patterns

For radio-marked birds, feeding was inferred from intermittent attenuation of telemetry signals. Locations of feeding ducks were related to a digital bathymetric map to determine the elevation below MLLW at which feeding occurred. (Elevation is the vertical distance of the sediment surface below the constant elevation of MLLW.) Although different duck species might dive at different tidal stages when water depth differed over a given location, our approach indicated use of the same elevation of sea floor by the different species. Despite a trend for SUSC to feed at elevations 45 to 52 cm lower than the scaup, the overall pattern was one of great overlap with no significant differences in subtidal elevations used by the 3 species (Fig. 6). We therefore assumed no partitioning of shoal habitat by elevation at subtidal depths.

Based on the Volume of Intersection Index, which accounts for both extent and intensity of space use,

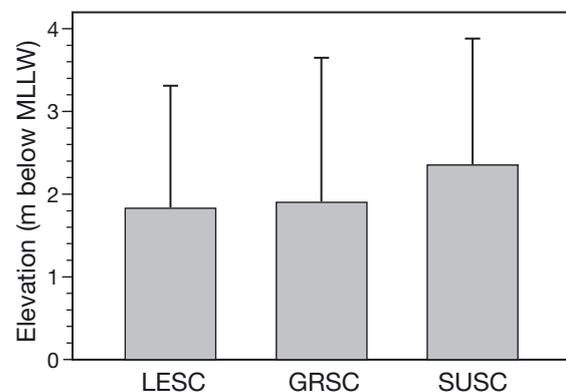


Fig. 6. *Aythya affinis*, *A. marila*, and *Melanitta perspicillata*. Mean ( $\pm 1$  SD) elevation (m below MLLW) at which radio-marked lesser scaup (LESC) and greater scaup (GRSC) in 1998 to 2001, and surf scoters (SUSC) in 2003 to 2005, fed by diving on the subtidal shoals of San Pablo Bay. Sample sizes were 35 LESG (74 dives), 36 GRSC (101 dives), and 50 SUSC (79 dives). There were no significant differences among species (nested ANOVA,  $p > 0.14$ ,  $F = 1.96$ )

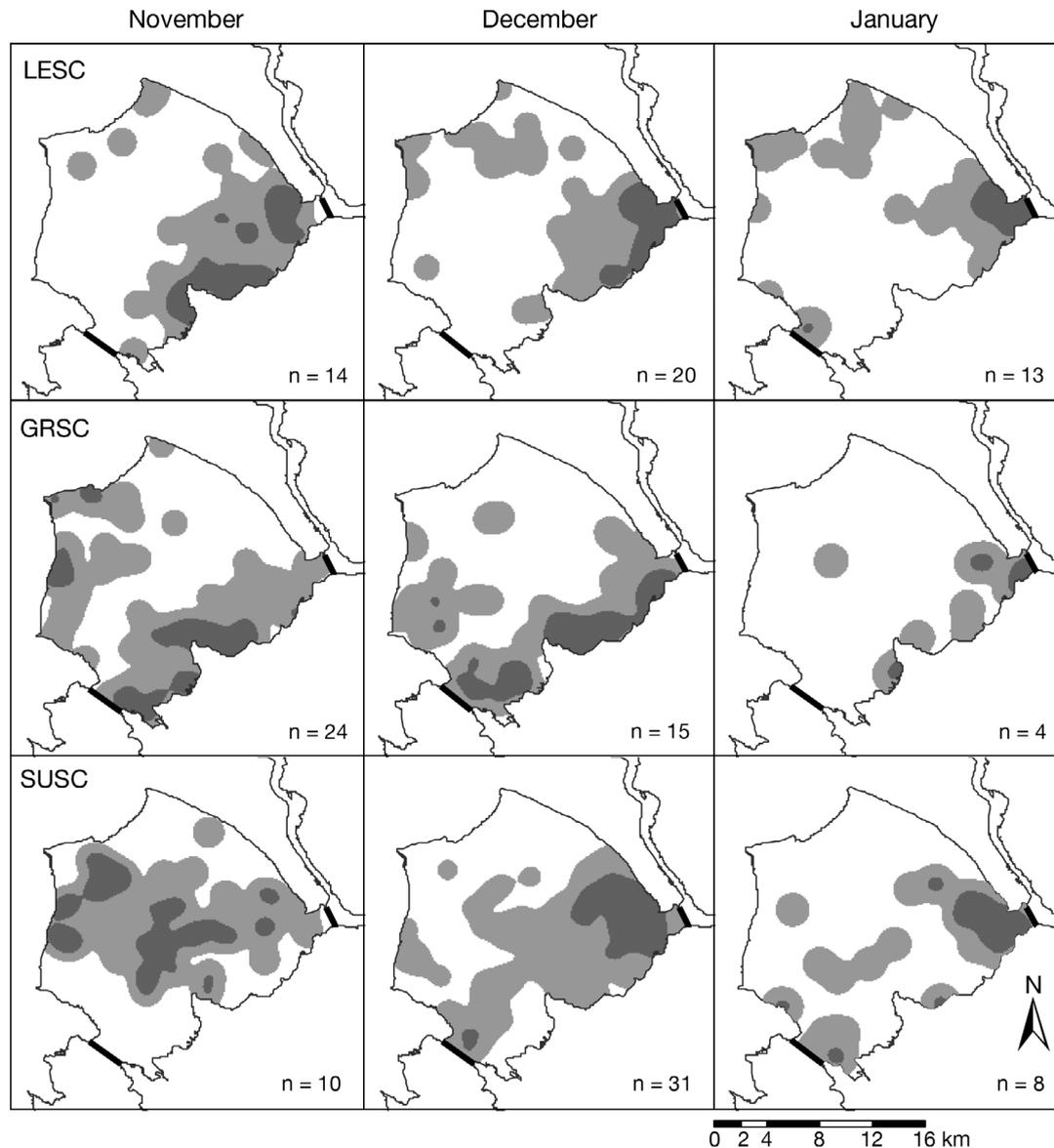


Fig. 7. *Aythya affinis*, *A. marila*, and *Melanitta perspicillata*. Spatial patterns of use intensity by radio-marked lesser scaup (LESC) and greater scaup (GRSC) in winter 1998–1999 and 1999–2000, and surf scoters (SUSC) in winter 2003–2004 and 2004–2005, in San Pablo Bay. Darker areas encompass 50%, and lighter areas 95%, of radio-locations. Five radio-locations per month were randomly selected for individuals for which there were  $\geq 5$  locations. Sample sizes are numbers of individuals included in each plot

areas occupied by radio-marked LES C overlapped by 11 to 44% with those used by GRSC, and 7 to 46% with those used by SUSC, depending on month (Fig. 7). Overlap between GRSC and SUSC ranged from 31 to 41%. Actual locations where the different species overlapped varied greatly between months, as did the dispersion of individual species, suggesting that each species was capable of using a wide range of areas. The tendency of SUSC to use slightly greater depths (Fig. 6) was most evident in November, but by January, use by all 3 species was concentrated near the inflow from Carquinez Strait into the

eastern side of the bay. Given this high variability, clear partitioning of different parts of the bay between these duck species was not apparent based on these data. Habitat use converged as food availability declined.

#### Chronology of numbers and departure from the bay

In most years, aerial counts of scaup (LESC and GRSC combined) in San Pablo Bay declined drama-

tically between fall to early winter (mid-October to early December) and late winter (January to February) (Fig. 8). In winter 1989–1990, scaup numbers were extremely high, with scaup counted in all regions of San Francisco Bay in mid-January representing 92% of all scaup counted in the Pacific Flyway 2 wk earlier (Accurso 1992). SUSC generally had much lower peak numbers but also declined very substantially by the end of January (Fig. 8). The chronology of departure of radio-marked scaup and scoters corresponded to aerial counts (Fig. S1 in the supplement). After leaving San Pablo Bay, almost no radio-marked scaup or scoters returned there, and the second increase in numbers in late February through March (Fig. 8) reflects spring migration from other areas (cf. De La Cruz et al. 2009).

### Threshold prey densities

Model estimates of threshold prey densities were largely unaffected by water depth, or by variations in shell length above 8 to 9 mm (Fig. 9). However, at lower shell lengths, the required prey density increased very rapidly (note that the highest density of *Corbula* measured was 41800 m<sup>-2</sup> at Stn 19 in 1993; see Fig. 3). Effects of the much smaller body size of LESC on overall energy costs were obviously important, with thresholds being appreciably lower for LESC than for the other species. GRSC and SUSC have similar body mass, and had similar patterns of threshold prey densities. However, despite the ability of SUSC to swim with wings as well as feet, their higher dive costs (W kg<sup>-1</sup>) and longer descent durations yielded higher overall energy costs and higher required prey densities than for GRSC.

### Uncertainty analyses

Uncertainty analyses for LESC indicated that, of the variables examined, feeding time per day was the most sensitive parameter affecting model estimates of profit per dive (Table 3). The shell length of *Corbula* was also important, as was the rate of

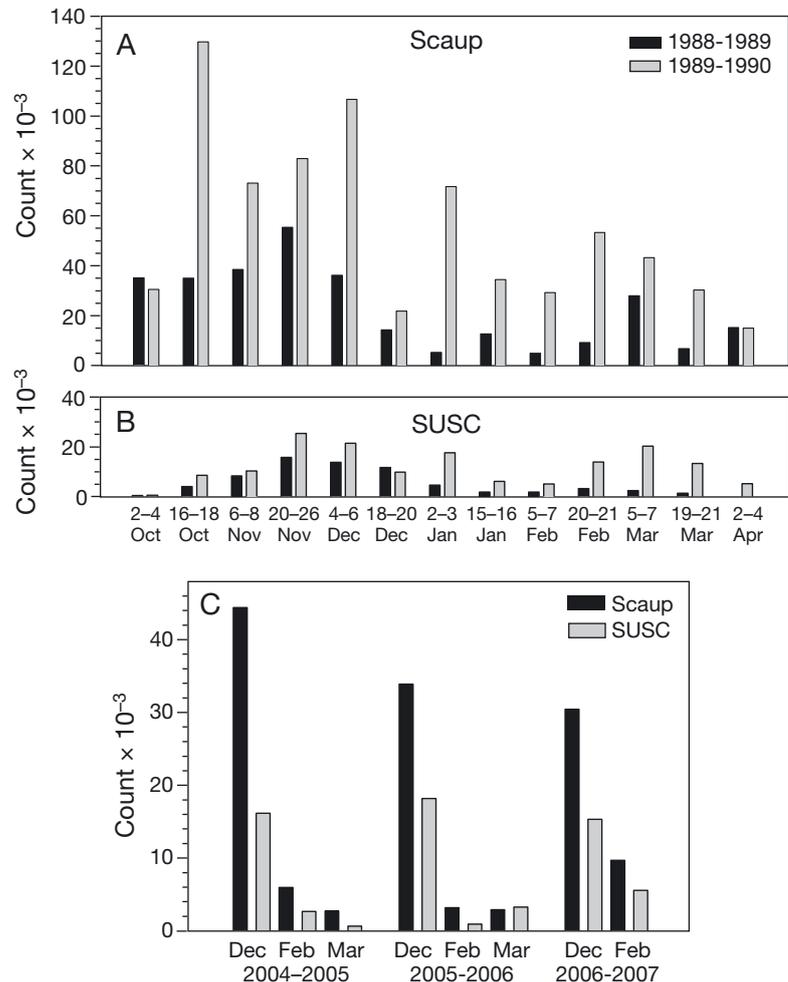


Fig. 8. *Aythya affinis*, *A. marila*, and *Melanitta perspicillata*. Aerial counts of (A,C) scaup (lesser and greater scaup combined) and (B,C) surf scoters (SUSC) in San Pablo Bay during different winter periods and years

diving during feeding periods. Variation in time spent foraging at the bottom had a much greater effect on profit per dive than did changes in intake rate at the bottom (functional response). Varying duration of flights from 0 to 29 min d<sup>-1</sup>, the latter considered a maximum for diving ducks that are often disturbed by humans (see the supplement), had negligible effect on required prey densities. The relative sensitivity of the model to these parameters depends strongly on the ranges over which they are varied—both RPSS and partial  $r^2$  can increase with greater ranges of variation, or if ranges are restricted to values over which a variable shows greatest change. For this reason, we selected ranges of variation that were realistic for each variable (Table 1).

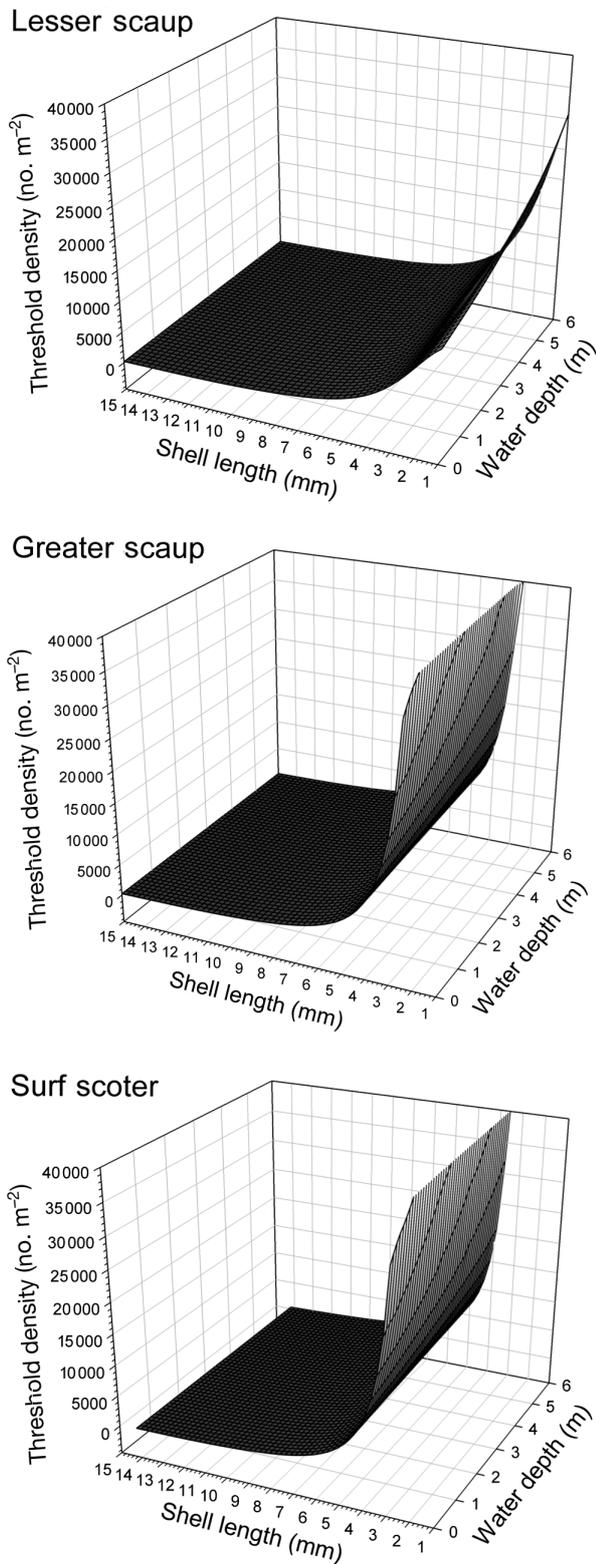


Fig. 9. *Aythya affinis*, *A. marila*, and *Melanitta perspicillata*. Effects of clam shell length and water depth on threshold prey densities required for profitable foraging, including daily overhead costs, for scaup and surf scoters

Table 3. *Aythya affinis*. Relative partial sums of squares (RPSS) and partial coefficients of determination (partial  $r^2$ ) for uncertainty analyses of the model to estimate profit per dive for lesser scaup in San Pablo Bay. For each of 300 iterations, a value for each parameter was randomly chosen from ranges in Table 1. Multiple  $R^2 = 0.92$  ( $p < 0.01$ )

Parameter	RPSS (%)	Partial $r^2$
Feeding time per day (min)	35.9	0.35
Mean <i>Corbula</i> shell length (mm)	29.8	0.25
Dive rate while feeding (dives min <sup>-1</sup> )	24.8	0.22
Time at the bottom per dive (s)	9.3	0.09
Functional response (prey s <sup>-1</sup> ) <sup>a</sup>	0.1	<0.01
Disturbance flight time per day (min)	0.1	<0.01

<sup>a</sup>Number of prey ingested per second at the bottom at a given prey density

### Proportions of area and *Corbula* stocks above threshold densities

In the fall benthic samples, mean ( $\pm 1$  SD) shell length of *Corbula* was  $9.1 \pm 4.0$  mm in 1990 ( $n = 3303$  clams),  $5.0 \pm 2.2$  mm in 1993 ( $n = 27939$ ),  $10.1 \pm 4.0$  mm in 1995 ( $n = 5934$ ), and  $8.4 \pm 3.9$  mm in 1999 ( $n = 2611$ ; Poulton et al. 2004). Rapid increase in profitability thresholds at shell lengths below 8 to 9 mm (Fig. 9) indicates that required densities were much higher in 1993. According to the model, the percentage of sampling stations (and area of San Pablo Bay) with high enough *Corbula* densities to support profitable foraging by the different duck species varied from 43–59% in 1990 to 78–85% in 1995 (Fig. 10A). The percentage of energy in *Corbula* standing stocks that was effectively unavailable to diving ducks due to profitability limitations ranged from 35% in 1995 to 66% in 1993 (Fig. 10B).

### Use-days with typical versus high duck populations

For scenarios of both very high (1989–1990) and more typical (1988–1989) diving duck numbers, food needs were determined for the entire winter and the subsequent influx of migrants during spring migration. For a year of moderate duck numbers (1988–1989), all 3 species appeared to be well below the estimated carrying capacity of the *Corbula* prey base for a range of prey densities found in different years (Table 4). However, in years of very high duck numbers (1989–1990) and low prey densities (1990), GRSC and SUSC were only about 6600 and 2200 birds below the maximum that could be supported throughout

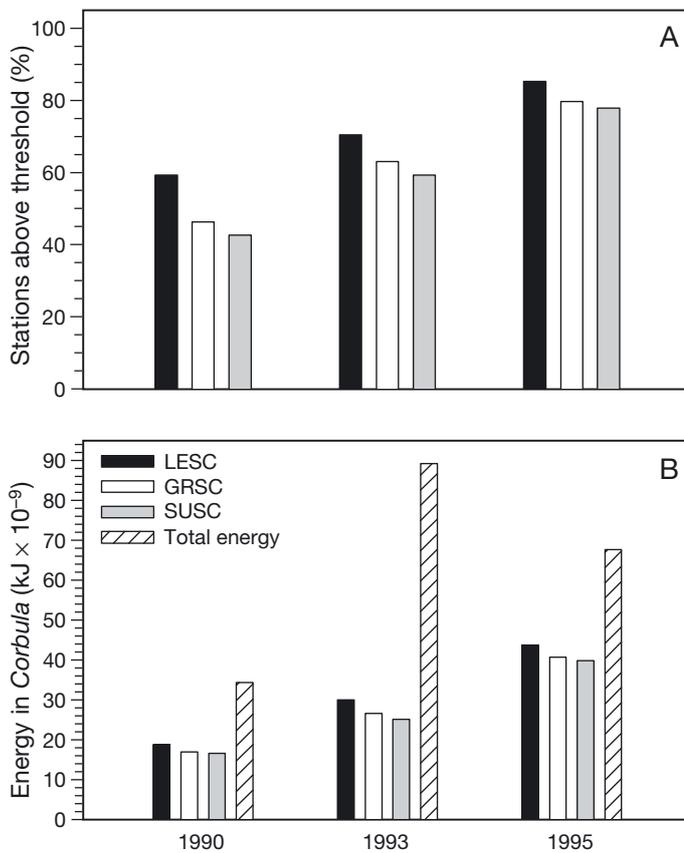


Fig. 10. *Aythya affinis*, *A. marila*, and *Melanitta perspicillata*. (A) Percentage of benthic sampling stations (see Fig. 3) at which densities of the clam *Corbula amurensis* were high enough to support profitable foraging by lesser scaup (LESC), greater scaup (GRSC), and surf scoters (SUSC) in September 1990, 1993, and 1995, and (B) energy in *Corbula* above profitability thresholds for the 3 duck species, compared to total energy in these clams

Table 4. *Aythya affinis*, *A. marila*, and *Melanitta perspicillata*. Mean daily numbers of diving ducks in San Pablo Bay based on bi-monthly aerial counts in October to mid-April 1988–1989 and 1989–1990 (Fig. 8), and additional numbers supportable in subtidal habitat (0 to –6 m MLLW) over this 197 d period if the prey base of *Corbula* clams was the same as in fall 1990, 1993, or 1995, and relative numbers of duck species were the same. Total numbers of scaup in aerial counts were assumed to be 44% LESG and 56% GRSC in 1988–1989, and 74% LESG and 26% GRSC in 1989–1990 (see ‘Materials and methods: Radio-telemetry and aerial surveys’). Numbers of use-days can be calculated by multiplying duck numbers by 197 d

Year of counts	Species	Mean daily number Oct to mid-Apr	Additional number supportable Oct to mid-Apr		
			1990	1993	1995
1988–1989	LESC	9993	32334	60245	84430
	GRSC	12822	26898	49963	82428
	SUSC	5408	12612	21888	37862
1989–1990	LESC	41074	30184	74664	121737
	GRSC	14431	6624	18774	36063
	SUSC	12146	2181	9556	22255

winter and spring migration, if relative numbers of all 3 duck species stayed the same.

### Impacts of ectothermic predators

Consumption by diving ducks versus ectothermic predators was compared for October through January for the combinations of moderate and high duck numbers and initial *Corbula* stocks (Tables S2 & S3 in the supplement at [www.int-res.com/articles/suppl/m479p251\\_supp.pdf](http://www.int-res.com/articles/suppl/m479p251_supp.pdf)). These comparisons were done for the fall and early winter, when these major ectothermic predators are present in the bay. Our estimates suggest that starry flounders, because of their high density and relatively high metabolic rate, are the major ectothermic competitors of diving ducks for *Corbula* clams during this period (Table 5). White sturgeon, with their large size and high metabolic rate, are also important. Dungeness crabs, whose abundance is relatively low during this season, had the least effect.

We compared numbers of ducks displaced by ectothermic consumption of *Corbula* (Table 5) to estimates of additional numbers of ducks that could be supported from October to January. For the winter of lowest prey availability (starting fall 1990), excess carrying capacity for different diving duck species would be reduced by 7 to 10% when duck populations are high (1989–1990) and by 4 to 6% when duck numbers are more typical (1988–1989). Estimated consumption by ectotherms would be about 17% of that by typical numbers of diving ducks observed in the bay in 1988–1989, and about 8% when duck numbers are very high as in 1989–1990. Thus, based on data from the mid-1970s to mid-1990s, impacts on the prey base by ectothermic predators during winter can add appreciably to the impacts of birds.

### DISCUSSION

Decreased body mass and fat, increased foraging effort, and major departures of these birds from San Pablo Bay appeared to result from food limitation. Moreover, for the 3 main avian benthivores in subtidal areas, the

Table 5. Estimated consumption of the clam *Corbula amurensis* by different ectothermic predators in subtidal areas of San Pablo Bay from October through January (123 d) based on values in Table S2 in the supplement ([www.int-res.com/articles/suppl/m476p251\\_supp.pdf](http://www.int-res.com/articles/suppl/m476p251_supp.pdf)), and resulting reduction in numbers of diving ducks that could be supported if relative numbers of duck species are the same as in 1988–1989 and 1989–1990, and the prey base is the same as in fall 1990 (see Table S3 in the supplement)

Predator	Calculated value	
<b>Ectotherms</b>	<b><i>Corbula</i> consumed (kJ)</b>	
White sturgeon	233335904	
Starry flounder	501083107	
Dungeness crab	40 mm	668663
	80 mm	601598
Total	735689272	
<b>Ducks</b>	<b>No. displaced by ectotherms</b>	
	1988–1989	1989–1990
Lesser scaup	2135	4139
Greater scaup	2740	1454
Surf scoter	1278	1016

overall pattern was substantial niche overlap and opportunistic use of the dominant prey species. These results accord with observations and theory suggesting that when certain prey taxa are far more profitable than others, similar predators may converge on those taxa until they are depleted below profitable levels (Pöysä 1986, Scheffer & van Nes 2006).

Nevertheless, energy costs associated with differing body size, locomotor mode, and dive behavior resulted in gradations of threshold prey densities required for profitable foraging: SUSC became food limited at higher prey densities than GRSC, which in turn were limited at higher prey densities than LESC. Also, as the prey base declines or numbers of ectothermic predators increase, such predators may start to compete with SUSC and the other duck species. Estimates of additional duck use-days supportable (Table 4) assumed that all *Corbula* present above threshold densities throughout San Pablo Bay can be readily located by the ducks, and that ectothermic predators have negligible impacts on the prey base—both these conditions are unlikely. Thus, it appears that in years of high duck populations and low prey availability, GRSC and especially SUSC could exceed the effective carrying capacity of San Pablo Bay over winter.

### Species differences in profitability thresholds

Differences in modeled profitability thresholds between duck species depended on energy costs.

LESC are 20 to 26% smaller than SUSC and GRSC, which are similar in body mass (Fig. 4). However, based on measurements in the same dive tank and respirometer, mass-specific costs of white-winged scoters ( $W \text{ kg}^{-1}$ ) were 16% higher for descent (12.2 versus 10.5) and 33% higher for bottom foraging (13.4 versus 10.1) than for LESC (Richman & Lovvorn 2008; see supplement). Moreover, the higher descent cost of scoters is applied over longer descent times: for a dive depth of 2 m in tanks, descent duration of white-winged scoters (4.4 s) was 63% longer than for LESC (2.7 s; Lovvorn 1994, Richman & Lovvorn 2008). The scaup also differed from SUSC in foraging behavior. During visual observations in the field, SUSC dove less frequently both throughout daylight hours and during feeding periods, with longer dive durations (Table S1 in the supplement).

The above differences suggest that for diving ducks in San Pablo Bay, the often-observed superiority of smaller species in exploitative competition (Persson 1985) can result from a combination of metabolic, locomotor, and behavioral traits. Aggressive interactions were very rarely observed. Thus, greater effectiveness in exploitative competition by the smaller species (LESC) was not offset (at least overtly) by superiority in interference competition by the larger species.

### Profitability thresholds, habitat shifts, and foraging aggression

Estimating carrying capacity in terms of energy balance requires identifying thresholds of food density above which energy gains during foraging exceed total daily costs. Threshold foraging behavior has been observed in diverse taxa from seabirds, whales, and basking sharks *Cetorhinus maximus* feeding on fish and zooplankton in the water column (Piatt 1990, Piatt & Methven 1992, Sims 1999); to crabs, rays, and shorebirds consuming nearshore benthic prey (Hines et al. 1997, Stillman et al. 2005, Seitz et al. 2008); to ducks and swans feeding on seeds, belowground plant tubers, and mussels (van Eerden 1984, Mitchell et al. 1994, De Leeuw 1999). For basking sharks feeding on zooplankton, and for diving ducks and swans feeding on belowground tubers, 'giving-up' densities below which the animals cease to forage have corresponded well with predicted thresholds of profitability (cf. Lovvorn & Gillingham 1996 and Sponberg & Lodge 2005, Sims 1999, Nolet et al. 2006).

However, the fact that shorebirds often leave 50% or more of initial prey stocks unexploited when they stop using an area suggests that the birds depart well before available stocks are depleted (Goss-Custard et al. 2006, Stillman & Goss-Custard 2010). In common eiders *Somateria mollissima* in the Dutch Wadden Sea, mass starvation and shifts to alternative habitats occurred when prey stocks were 4.7 times higher than estimated needs of the eiders (Camphuysen et al. 2002). In our study, 35 to 66% of the energy in initial *Corbula* stocks occurred at densities below profitability thresholds, so large percentages of food remaining upon departure do not necessarily represent available resources. Nevertheless, our model indicated that an additional large quantity of prey remained above threshold densities when most ducks left San Pablo Bay.

For both shorebirds and dispersing rodents, so-called 'presaturation dispersal' from feeding areas that appear to remain adequate has been attributed to intraspecific aggression by dominant individuals (Grant 1978, Stillman & Goss-Custard 2010). One expects this dominance effect to increase as food becomes more clumped, long-lasting, and spatially predictable, so that patches are of high value, small enough to be defended by dominant individuals, and cannot be discovered and depleted quickly by subordinates before dominant animals can displace them. European oystercatchers *Haematopus ostralegus* feed during low tide on easily located mussels, which are often attached in clumps to hard substrates that protrude above soft sediments exposed at low tide. These clumps are quite valuable, spatially predictable, small enough to be defended, and require appreciable time and effort for the birds to pry open or break the shells (Goss-Custard et al. 1993). As expected under these conditions, foraging aggression is common. Models and some data indicate that subordinate oystercatchers may starve when food stocks are still adequate to meet total energy needs of the population, so that up to 8 times the calculated limiting amount is required for all birds to survive winter in good condition (Goss-Custard et al. 2004). In such cases, failure to consider effects of dominance behavior could result in serious overestimates of effective carrying capacity.

### Search costs, antipredator behavior, and satisficing

However, for some species, foraging aggression does not explain departure from habitats when food stocks are still well above thresholds required to

meet per capita energy needs. In bottom-feeding diving ducks, foraging aggression in non-breeding habitats occurs only under certain circumstances, such as feeding on an exceptionally valuable and clumped food. For example, foraging swans can incidentally unearth many deeply buried tubers that are otherwise inaccessible to ducks; thus, swans can themselves become defendable 'patches' of available food. In such cases, aggression among ducks can appear abruptly with no change in diet but only in the defendability of the same food in the same area (Lovvorn 1989). However, in 120 h of observations over 3 winters, we observed no foraging aggression among scaup or scoters in San Pablo Bay (Poulton et al. 2002, present study).

Instead, we believe that these diving ducks left San Pablo Bay 'prematurely' because they could not find or access all patches above threshold densities that occurred throughout the bay. Especially in these highly turbid waters, avian benthivores cannot locate their infaunal foods from the air or water surface, but must search within the sediments by touch while holding their breath and diving to the bottom. The high cost of this search method is a main reason that diving ducks are so attracted to hunting decoys—it requires far less effort to find a flock that has already located an adequate food patch. GRSC collected in late winter had eaten many *Corbula* 2–4 mm long (Fig. 5, Table 2); however, densities estimated as high enough for profitable foraging on those sizes ( $>10\,000\text{ m}^{-2}$ , Fig. 9) occurred at only a third of 54 stations in 1993, and at no stations in 1990 and 1995. Without cueing on flocks that have already located high-density patches, the cost of searching for such patches as their incidence declines may become prohibitive.

Other studies indicate that, owing to incomplete information, some foragers will remain in inferior patches where densities may be drawn down below profitable thresholds well before many adequate patches are depleted (Beauchamp et al. 1997, Amano et al. 2006). Field experiments on shorebirds and rays have shown that if the scale of patchiness is too small, these predators may not detect high prey densities and therefore leave many good patches unexploited (Hines et al. 1997, Santos et al. 2009). Even when consumers can detect small patches, if the patches are widely and unpredictably dispersed, the high search costs may increase required threshold densities, leading to early departure from the habitat.

At 6 sites in subtidal areas of San Pablo Bay, density of *Corbula* at each station along transects was sampled at 1 m increments to a distance of 5 m. At 4 sites,

there was correlation among samples at scales of 1 to 5 m, while at 2 sites, there was almost no correlation among samples at these scales (Fig. 6a in Poulton et al. 2004). At larger scales, there was correlation of prey densities at a distance of 100 m along 1400 m transects at all sites, but no consistent pattern of correlation at scales >100 m. These transect sites were selected for being known feeding areas of scaup; however, at either small (1 to 5 m) or large (100 to 1400 m) scales, an individual forager could spend much time searching at random before encountering a patch with profitable prey density. In a coastal lake in the Netherlands, GRSC and tufted ducks *Aythya fuligula* often did not search out and deplete patches with exceptional prey density. Instead, they mainly used areas of generally high prey density that were consistently frequented by flocks (van Eerden et al. 1997). Even when flocking does not increase overall intake rate, it can decrease variation in intake and the risk of finding no food over short periods (Thompson et al. 1974, Amano et al. 2006).

Also, because diving ducks cannot avoid detection in open water and cannot take off abruptly from the water surface, they typically form dense flocks and use the confusion effect to thwart avian predators (Lovvorn 1989). This tactic does not work unless the attacked species remains near concentrations of conspecifics. Thus, experience with predatory gulls and raptors over the annual cycle may inhibit diving ducks and other birds of open habitats from searching for food away from large flocks (Page & Whitacre 1975). Models have shown that predation attempts need not be frequent to elicit strong aggregative behavior (Stinson 1980), with important nonlethal effects on foraging.

In summary, high energy costs of searching and innate, antipredator flocking behavior may strongly limit exploitation of many patches that would otherwise be profitable (Thompson et al. 1974). Given that shorebirds also form flocks and disperse less widely in the presence of avian predators (Whitfield 1988), reported instances of incomplete food exploitation by shorebirds may result partly from antipredator behavior and incomplete searching. Similar constraints may cause a wide range of endotherm and ectotherm taxa, especially those that aggregate to invoke the confusion effect (Hobson 1978), to emigrate from habitats well before depleting food to estimated carrying capacity.

Moreover, animals might not be 'satisficers' which continue feeding in an area as long as energy balance remains positive, but instead might seek to maximize energy intake by leaving sites whenever intake rate falls below that in alternative areas (Lovvorn &

Gillingham 1996). The energy maximization (marginal value) scheme presumes updated knowledge of alternative resources in a complex of feeding areas, where prey density can change greatly between years, among sites, and through winter with variable and ongoing depletion by other predators. Given the high costs of searching in diving ducks, and their apparent inability to locate many good patches within the same area (van Eerden et al. 1997, Camphuysen et al. 2002), we expect that knowledge of alternative feeding sites is often poor and favors a satisficing strategy (cf. Stillman et al. 2005, Amano et al. 2006).

### Effects of ectothermic predators

For a prey base and predator densities typical of the early 1990s, our model suggests that consumption of *Corbula* by ectothermic predators from October through January was about 17% of that consumed by diving ducks. In years of very high duck numbers such as 1989–1990, and low prey availability as in 1990, ectothermic predators may decrease the excess carrying capacity for ducks by 7 to 10%.

In San Francisco Bay, some analyses have emphasized control of the bivalve prey base by periodic invasion or irruption of ectothermic predators (Cloern et al. 2007), whereas others have argued that birds may be a more important regulating factor (Thompson et al. 2008). The answer to this question is important from our perspective because it determines whether carrying capacity estimates based only on birds will be valid. If we did not do this analysis, our calculation that much food remains when the ducks abandon San Pablo Bay might simply result from lack of accounting for consumption by ectotherms. Although our estimates are approximate, they clearly eliminate this alternative explanation in this case. Future studies should work toward better accounting of the joint impacts of endothermic and ectothermic predators under a range of conditions.

### Food dispersion, behavior, and carrying capacity

As shown in this study and others, animals often do not exploit a substantial fraction of food above local profitability thresholds before abandoning an area; thus, carrying capacity can be overestimated if based solely on energetic profitability within patches. One explanation is that if adequate patches are widely and unpredictably dispersed, are difficult to find, and can be depleted quickly, the cost of searching for

them can be prohibitively high relative to benefits. On the other hand, if suitable patches are clumped, are not quickly depleted, and are thus economically defendable, socially subordinate animals may suffer negative energy balance even while the total amount of food is adequate for all population members. Aggregative behavior can exacerbate either of these effects, by reducing the effective area that an individual can search for good patches, or by compelling individuals to stay in flocks where they are excluded from good patches by dominant individuals (Thompson et al. 1974, Hobson 1978). Where foods are evenly dispersed and there is little aggregative or aggressive behavior, estimated and observed giving-up densities may be similar. Technically, both the costs of searching for rare and unpredictably dispersed food patches, and decreased energy intake owing to aggression or antipredator behavior, could be included in energetics calculations of threshold food densities. However, such aspects of energy budgets are quite difficult to quantify. Nevertheless, this general conceptual framework may help to identify situations where thresholds of energetic profitability are likely to overestimate the realized carrying capacity.

### Conservation and carrying capacity for multiple species

For many conservation programs, a key question is whether further habitat loss, either through climate change or direct human impacts, will cause population declines of any of a suite of coexisting species. In many cases, conservation of a particular species of interest requires considering a diverse interacting assemblage with which it shares resources. Although these problems are difficult to address quantitatively, management decisions will nonetheless be made. We have shown that calculations of threshold prey densities can indicate the species most vulnerable to food declines. However, estimates of total habitat needed await better insight into factors that determine the amount of food that is not depleted before departure of the animals.

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### LITERATURE CITED

- Accurso LM (1992) Distribution and abundance of wintering waterfowl on San Francisco Bay, 1988–1990. MSc thesis, Humboldt State University, Arcata, CA
- Amano T, Ushiyama K, Moriguchi S, Fujito G, Higuchi H (2006) Decision-making in group foragers with incomplete information: test of individual-based model in geese. *Ecol Monogr* 76:601–616
- Beauchamp G, Bélisle M, Giraldeau LA (1997) Influence of conspecific attraction on the spatial distribution of learning foragers in a patchy habitat. *J Anim Ecol* 66:671–682
- Camphuysen CJ, Berrevoets CM, Cremers HJWM, Dekinga A and others (2002) Mass mortality of common eiders (*Somateria mollissima*) in the Dutch Wadden Sea, winter 1999/2000: starvation in a commercially exploited wetland of international importance. *Biol Conserv* 106:303–317
- Cloern JE, Jassby AD, Thompson JK, Hieb KA (2007) A cold phase of the East Pacific triggers new phytoplankton blooms in San Francisco Bay. *Proc Natl Acad Sci USA* 104:18561–18565
- De La Cruz SEW, Takekawa JY, Wilson MT, Nysewander DR and others (2009) Spring migration routes and chronology of surf scoters (*Melanitta perspicillata*): a synthesis of Pacific Coast studies. *Can J Zool* 87:1069–1086
- De Leeuw JJ (1999) Food intake rates and habitat segregation of tufted duck *Aythya fuligula* and scaup *Aythya marila* exploiting zebra mussels *Dreissena polymorpha*. *Ardea* 87:15–31
- Eggleston DB, Lipcius RN, Hines AH (1992) Density-dependent predation by blue crabs upon infaunal clam species with contrasting distribution and abundance patterns. *Mar Ecol Prog Ser* 85:55–68
- Friedlaender AS, Johnston DW, Fraser WR, Burns J, Halpin PN, Costa DP (2011) Ecological niche partitioning of sympatric krill predators around Marguerite Bay, Western Antarctic Peninsula. *Deep-Sea Res II* 58:1729–1740
- Goss-Custard JD, West AD, le V dit Durell SEA (1993) The availability and quality of the mussel prey (*Mytilus edulis*) of oystercatchers (*Haematopus ostralegus*). *Neth J Sea Res* 31:419–439

- Goss-Custard JD, Stillman RA, West AD, Caldow RWG, Triplet P, le V dit Durell SEA, McGroarty S (2004) When enough is not enough: shorebirds and shellfishing. *Proc R Soc Lond B Biol Sci* 271:233–237
- Goss-Custard JD, West AD, Yates MG, Caldow RW and others (2006) Intake rates and the functional response in shorebirds (Charadriiformes) eating macro-invertebrates. *Biol Rev Camb Philos Soc* 81:501–529
- Grant PR (1978) Dispersal in relation to carrying capacity. *Proc Natl Acad Sci USA* 75:2854–2858
- Hines AH, Whitlatch RB, Thrush SF, Hewitt JE, Cummings VJ, Dayton PK, Legendre P (1997) Nonlinear foraging response of a large marine predator to benthic prey: eagle ray pits and bivalves in a New Zealand sandflat. *J Exp Mar Biol Ecol* 216:191–210
- Hobson ES (1978) Aggregating as a defense against predators in aquatic and terrestrial environments. In: Reese ES, Lighter FJ (eds) *Contrasts in behavior*. Wiley, New York, NY, p 219–234
- Kohlhorst DW, Botsford LW, Brennan JS, Cailliet GM (1991) Aspects of the structure and dynamics of an exploited central California population of white sturgeon (*Acipenser transmontanus*). In: Williot P (ed) *Accipenser: Actes du Premier Colloque International sur l'Esturgeon*, Bordeaux, 3–6 October 1989. CEMAGREF-DOCA, Bordeaux, p 277–293
- Laidre KL, Jameson RJ, Jeffries SJ, Hobbs RC, Bowlby CE, VanBlaricom GR (2002) Estimates of carrying capacity for sea otters in Washington state. *Wildl Soc Bull* 30: 1172–1181
- Lewis TL, Esler D, Boyd WS, Zydalis R (2005) Nocturnal foraging behavior of wintering surf scoters and white-winged scoters. *Condor* 107:637–647
- Lovvorn JR (1989) Food defendability and antipredator tactics: implications for dominance and pairing in canvasbacks. *Condor* 91:826–836
- Lovvorn JR (1994) Biomechanics and foraging profitability: an approach to assessing trophic needs and impacts of diving ducks. *Hydrobiologia* 279–280:223–233
- Lovvorn JR, Gillingham MP (1996) Food dispersion and foraging energetics: a mechanistic synthesis for field studies of avian benthivores. *Ecology* 77:435–451
- Lovvorn JR, Grebmeier JM, Cooper LW, Bump JK, Richman SE (2009) Modeling marine protected areas for threatened eiders in a climatically changing Bering Sea. *Ecol Appl* 19:1596–1613
- Luo J, Hartman KJ, Brandt SB, Cerco CF, Rippetoe TH (2001) A spatially-explicit approach for estimating carrying capacity: an application for the Atlantic menhaden (*Brevoortia tyrannus*) in Chesapeake Bay. *Estuaries* 24: 545–556
- Millspaugh JJ, Gitzen RA, Kernohan BJ, Larson MA, Clay CL (2004) Comparability of three analytical techniques to assess joint space use. *Wildl Soc Bull* 32:148–157
- Mitchell CA, Custer TW, Zwank PJ (1994) Herbivory on shoalgrass by wintering redheads in Texas. *J Wildl Manag* 58:131–141
- Nolet BA, Gyimesi A, Klaassen RHG (2006) Prediction of bird-day carrying capacity on a staging site: a test of depletion models. *J Anim Ecol* 75:1285–1292
- Orsi JJ (1999) Report on the 1980–1995 fish, shrimp, and crab sampling in the San Francisco Estuary, California. Calif Dept Fish Game, Stockton, CA
- Page G, Whitacre DF (1975) Raptor predation on wintering shorebirds. *Condor* 77:73–83
- Painter RE (1966) Zoobenthos of San Pablo and Suisun Bays. Calif Dept Fish Game. Fish Bull 133:40–56
- Parchaso F, Thompson JK (2002) Influence of hydrologic processes on reproduction of the introduced bivalve *Potamocorbula amurensis* in northern San Francisco Bay, California. *Pac Sci* 56:329–345
- Persson L (1985) Asymmetrical competition: are larger animals competitively superior? *Am Nat* 126:261–266
- Peterson HA, Vayssières M (2010) Benthic assemblage variability in the upper San Francisco Estuary: a 27-year retrospective. *San Francisco Estuary & Watershed Sci* 8(1). Available from <http://escholarship.org/uc/item/4d0616c6>
- Piatt JF (1990) The aggregative response of common murre and Atlantic puffins to schools of capelin. *Stud Avian Biol* 14:36–51
- Piatt JF, Methven DA (1992) Threshold foraging behavior of baleen whales. *Mar Ecol Prog Ser* 84:205–210
- Poulton VK, Lovvorn JR, Takekawa JY (2002) Clam density and scaup feeding behavior in San Pablo Bay, California. *Condor* 104:518–527
- Poulton VK, Lovvorn JR, Takekawa JY (2004) Spatial and overwinter changes in clam populations of San Pablo Bay, a semiarid estuary with highly variable freshwater inflow. *Estuar Coast Shelf Sci* 59:459–473
- Pöysä H (1986) Foraging niche shifts in multispecies dabbling duck (*Anas* spp.) feeding groups: harmful and beneficial interactions between species. *Ornis Scand* 17: 333–346
- Richman SE, Lovvorn JR (2004) Relative foraging value to lesser scaup ducks of native and exotic clams from San Francisco Bay. *Ecol Appl* 14:1217–1231
- Richman SE, Lovvorn JR (2008) Costs of diving by wing and foot propulsion in a sea duck, the white-winged scoter. *J Comp Physiol B* 178:321–332
- Richman SE, Lovvorn JR (2009) Predator size, prey size, and threshold food densities of diving ducks: does a common prey base support fewer large animals? *J Anim Ecol* 78: 1033–1042
- Santos CD, Saraiva S, Palmeirim JM, Granadeiro JP (2009) How do waders perceive buried prey with patchy distributions? The role of prey density and size of patch. *J Exp Mar Biol Ecol* 372:43–48
- Scheffer M, van Nes EH (2006) Self-organized similarity, the evolutionary emergence of groups of similar species. *Proc Natl Acad Sci USA* 103:6230–6235
- Seitz RD, Lipcius RN, Knick KE, Seebo MS, Long WC, Brylawski BL, Smith A (2008) Stock enhancement and carrying capacity of blue crab nursery habitats in Chesapeake Bay. *Rev Fish Sci* 16:329–337
- Sims DW (1999) Threshold foraging behavior of basking sharks on zooplankton: life on an energetic knife-edge? *Proc R Soc Lond B Biol Sci* 266:1437–1443
- Sponberg AF, Lodge DM (2005) Seasonal belowground herbivory and a density refuge from waterfowl herbivory for *Vallisneria americana*. *Ecology* 86:2127–2134
- Stillman RA (2008) MORPH—An individual-based model to predict the effect of environmental change on foraging animal populations. *Ecol Model* 216:265–276
- Stillman RA, Goss-Custard JD (2010) Individual-based ecology of coastal birds. *Biol Rev Camb Philos Soc* 85: 413–434
- Stillman RA, West AD, Goss-Custard JD, McGroarty S and others (2005) Predicting site quality for shorebird communities: a case study on the Humber estuary, UK. *Mar Ecol Prog Ser* 305:203–217

- Stinson CH (1980) Flocking and predator avoidance: models of flocking and observations on the spatial dispersion of foraging winter shorebirds (Charadrii). *Oikos* 34:35–43
- Thompson JK, Nichols NH (1981) Benthic macrofaunal biomass of San Francisco Bay, California: January/February and August 1973. US Geol Surv Open-File Rep 81-1331
- Thompson WA, Vertinsky I, Krebs JR (1974) The survival value of flocking in birds: a simulation model. *J Anim Ecol* 43:785–820
- Thompson JK, Koseff JR, Monismith SG, Lucas LV (2008) Shallow water processes govern system-wide phytoplankton bloom dynamics: a field study. *J Mar Syst* 74: 153–166
- van Eerden MR (1984) Waterfowl movements in relation to food stocks. In: Evans PR, Goss-Custard JD, Hale WG (eds) Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge, p 84–100
- van Eerden MR, de Leeuw JJ, Slager B bij de Vaate A (1997) A field test of the carrying capacity concept in wintering diving ducks: Do high foraging costs delimit exploitation of zebra mussels? In: van Eerden MR (ed) Patchwork: patch use, habitat exploitation and carrying capacity for water birds in Dutch freshwater wetlands. Rijkswaterstaat, Lelystad, p 283–316
- Werner EE (1979) Niche partitioning by food size in fish communities. In: Clepper H (ed) Predator–prey systems in fisheries management. Sport Fishing Institute, Washington, DC, p 311–322
- Whitfield DP (1988) Sparrowhawks *Accipiter nisus* affect the spacing behaviour of wintering turnstone *Arenaria interpres* and redshank *Tringa totanus*. *Ibis* 130:284–287
- Zwarts L, Wanink JH (1993) How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. *Neth J Sea Res* 31:441–476

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