Effects of Wetland Management on Carrying Capacity of Diving Ducks and Shorebirds in a Coastal Estuary

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Abstract.—With global loss of natural wetlands, managed wetlands increasingly support energy requirements for wintering shorebirds and waterfowl. Despite numerous studies of avian bioenergetics in freshwater systems, less is known of the energetic capacity of estuarine systems. In San Francisco Bay, managed saline ponds converted from former commercial salt evaporation ponds form part of the largest wetland restoration project on the Pacific coast of North America. A daily-ration model was applied to assess carrying capacity for diving ducks and shorebirds during four winter seasons (2007-2010) in seasonal and circulation ponds, each in two salinity classes. Diving ducks comprised an estimated 35,450 ± 1,559 ($\bar{x}$ ± SE) in average years and 45,458 ± 1,653 in peak years with > 95% in circulation ponds. Shorebirds comprised 64,253 ± 14,838 ($\bar{x}$ ± SE) in average years and 108,171 ± 4,854 in peak years with > 64% in seasonal ponds. Macroinvertebrate energy density was highest in mesohaline (5-30 ppt) circulation ponds and lowest in seasonal ponds for both guilds. Energy requirements for diving ducks in mesohaline followed by low-hyperhaline (30-80 ppt) circulation ponds were mostly met by available prey energy. Available energy for shorebirds was substantially less than they required in seasonal ponds but exceeded their needs in mesohaline circulation ponds. Mesohaline circulation ponds supported 9,443 ± 1,649 ($\bar{x}$ ± SE) shorebird use-days·ha^{-1} of accessible habitat and 2,297 ± 402 diving duck use-days·ha^{-1} of accessible habitat, twice the capacity of low-hyperhaline circulation ponds and greater than five times that of seasonal ponds for both guilds. Our results indicated that reducing salinity to mesohaline levels and altering water depth to increase accessibility substantially increased energy available for these species in estuarine managed ponds. *Received 4 March 2013, accepted 8 July 2013.*

Key words.—benthic invertebrates, carrying capacity, diving ducks, estuarine, managed wetlands, salt ponds, San Francisco Bay, shorebirds, supratidal.

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With global loss and degradation of natural wetlands during the past two centuries, managed wetlands have become critical to support energy requirements for millions of migrating shorebirds and waterfowl (Shuford *et al.* 1998; Elphick 2000; Taft *et al.* 2002; Stralberg *et al.* 2011). Over several decades, moist-soil management that mimics the timing and duration of water levels in natural wetlands has been applied extensively across freshwater systems to promote growth of beneficial forage plants for herbivorous waterfowl such as numerous dabbling duck species (Heitmeyer 1989; Anderson and Smith 1999; Taft *et al.* 2002). Recent efforts have focused on managing water levels to enhance invertebrate abundances for waterfowl and shorebirds to support multi-species management goals (Safran *et al.* 1997; Anderson and Smith 1999, 2000; Bolduc and Afton 2004). However, despite success in implementing management practices that promote available forage for migratory waterbirds in freshwater or agricultural systems, less is known about managing wetlands to support energy needs for waterbirds in estuarine systems that support high waterbird abundances (Weber and Haig 1996; Stralberg *et al.* 2011).

Estuarine intertidal and subtidal mudflats provide prey resources for diving ducks

and shorebirds that forage on benthic invertebrates, whereas supratidal areas provide roosting and foraging habitat for shorebirds when intertidal mudflats are inundated at high tide (Warnock *et al.* 2002; Dias 2009). Supratidal habitats such as diked salt ponds, salt pans, and managed wetlands have been shown to supplement daily energy intake for foraging shorebirds in estuaries worldwide (Velasquez and Hockey 1992; Masero and Pérez-Hurtado 2001; Dias 2009; Sripanomyom *et al.* 2011). Salt ponds were used by foraging birds throughout the tidal cycle suggesting preferential foraging even when mudflats were exposed (Dias 2009). Supratidal habitats also contributed significantly to maintain waterbird energy intake when adjacent to mudflats of high productivity (Velasquez 1992; Velasquez and Hockey 1992; Weber and Haig 1996; Masero and Perez-Hurtado 2001). In one study, benthic invertebrates had greater densities in managed estuarine wetlands compared with adjacent natural mudflats (Weber and Haig 1996). Invertebrate composition differs across salinity gradients ranging from mesohaline to hyperhaline (Herbst 2006; Takekawa *et al.* 2009), and less is known about management of estuarine wetlands to enhance benthic invertebrate prey for waterbirds (Hands *et al.* 1991; Shuford *et al.* 1998).

San Francisco Bay is the largest estuary on the Pacific Coast of the USA and critically important for waterbird stopover and wintering habitat. San Francisco Bay harbors nearly 50% of the total population of several diving duck species during winter (Accurso 1992) and is a site of Hemispheric Importance for shorebirds (Myers *et al.* 1987). Restoration of tidal marshes and managed ponds converted from former commercial salt evaporation ponds form part of the largest wetland restoration project on the Pacific coast of North America. However, increased sediment demand for tidal marsh restoration, while expected to benefit tidal marsh species, could reduce the area of existing bay mudflats by up to 50% over 50 years (Brew and Williams 2010) with potential reduction in waterbird foraging resources (Lovvorn *et al.* 2013). Thus, management of salt ponds may provide critical supplemental foraging resources for waterbirds during the nonbreeding (winter and migration) seasons. However, no prior studies have estimated avian abundance or energy availability from benthic invertebrates in diked estuarine wetlands as a function of pond management regimes.

Our goal was to assess the carrying capacity of four types of South Bay Salt Pond managed ponds for diving ducks and shorebirds in winter. Our specific objectives were to: 1) estimate energy required by diving ducks and shorebirds that comprise > 95% of the bird community during the winter; 2) estimate the benthic invertebrate energy density by pond type; 3) estimate total energy available to birds by pond type; and 4) compare energy intake with total energy available to evaluate carrying capacity.

METHODS

Study Area

Our study area consisted of former salt production ponds that are part of the South Bay Salt Pond Restoration Project in South San Francisco Bay (37.42-37.62° N; 121.93-122.22° W; Fig. 1). Of 54 ponds, we excluded ponds that were breached or under construction. We also excluded circulation ponds maintained at an average salinity > 80 ppt, and seasonal ponds maintained at an average salinity > 150 ppt due to substantial changes that occur in the invertebrate community above these thresholds (Williams 1998; Takekawa *et al.* 2006). The remaining 46 ponds were divided into four categories based on conditions during winter 2007-2010 that served as a baseline immediately prior to the first phase of restoration actions (Fig. 1).

The four pond type categories were based on two pond management regimes, circulation and seasonal ponds, each in two salinity classes (Fig. 1). Circulation ponds intake, circulate, or discharge water directly to or from the Bay or adjacent sloughs. These ponds were maintained as the deepest ponds in the system and had water levels that fluctuated with muted tides. We classified 14 circulation ponds as mesohaline (5-30 ppt) and 12 ponds as low-hyperhaline (31-80 ppt) on the basis of the average 3-month winter salinity over 4 years. Seasonal ponds were hydrologically closed (no intake or discharge) with water exchange driven by seasonal rainfall and evaporation. These ponds were typically dry during the summer and became inundated with rainwater during the wet season (December to April). We classified 10 seasonal ponds as low-hyperhaline and 10 seasonal ponds as medium-hyperhaline (80-150 ppt).

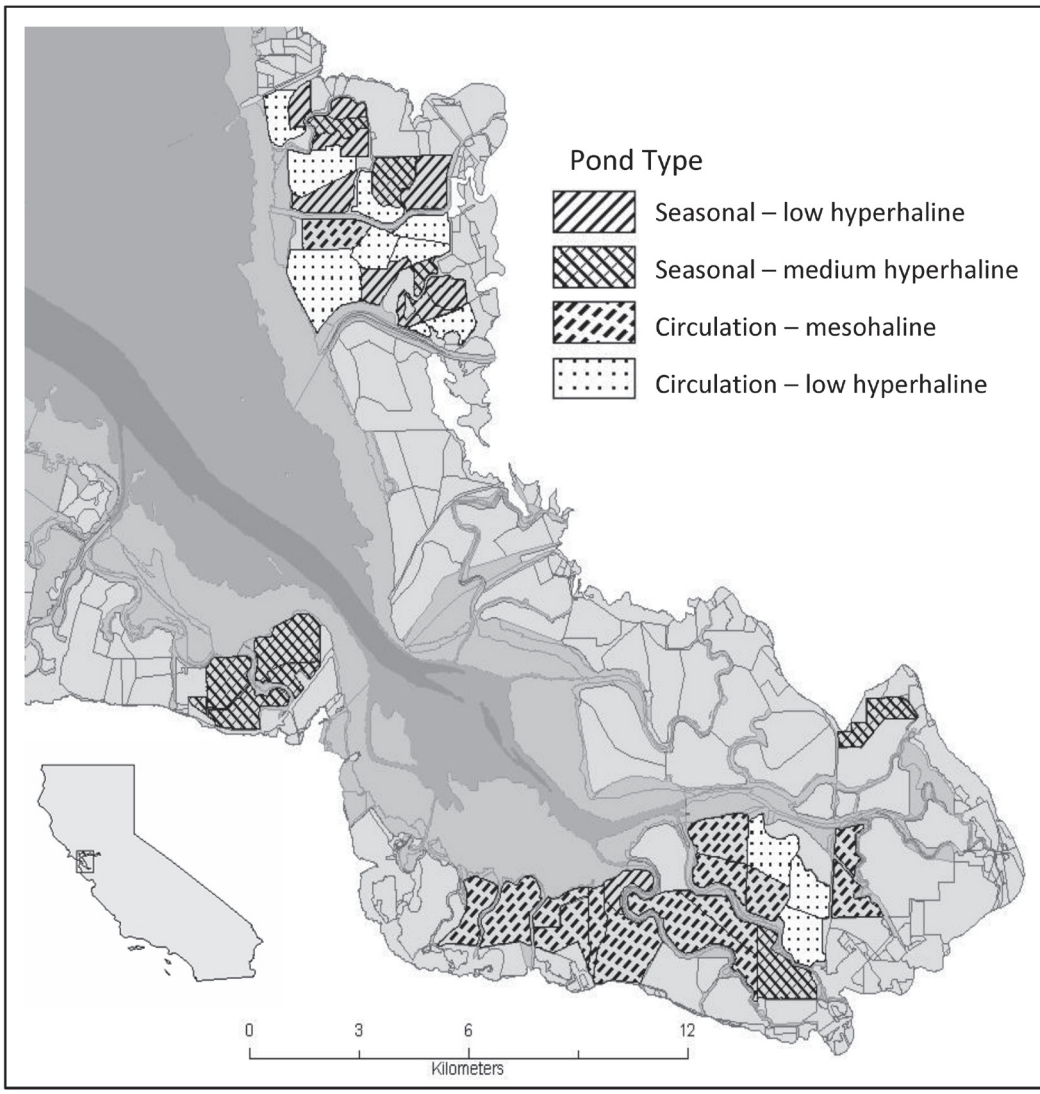

Figure 1. Map of the study area showing the San Francisco Bay area with 46 former salt production ponds in the South Bay considered in this study, classified into four pond types on the basis of management regime and salinity classes during the winters of 2007-2010. We defined salinity classes as mesohaline (< 30 ppt), low-hyperhaline (30-80 ppt), and medium-hyperhaline (80-150 ppt). Light to dark gray areas represents mudflats to deeper bay channels, and white, bordered areas represent active salt production, restored tidal marsh, or other types of management not considered in this study.

We measured conductivity (Hydrolab Minisonde) at < 70 ppt, and at greater salinities we measured specific gravity (Ertco hydrometer) scaled for the appropriate range and corrected for temperature. Salinity ranges were based on a prior study that showed similarities of invertebrate and vertebrate communities within these classes (Takekawa *et al.* 2006).

Avian Abundances and Energy Requirements

We conducted monthly (December, January, February) waterbird surveys during four winter seasons (2007-2010). To avoid double counting, we recorded birds within 250-m × 250-m (6.25-ha) grids within ponds; observers used existing landmarks and physical features to identify the grid cell locations of each bird (Takekawa *et al.* 2006). Observers conducted counts from vantage points on pond levees. We conducted surveys at high tide (> 1.2 meters Mean Higher High Water), which we assumed represented the maximum abundances of shorebirds within salt ponds due to inundation of adjacent mudflats (Warnock *et al.* 2002). We summed birds across grids and ponds by pond type, month, and year,

and then averaged over months (n = 12 surveys) to obtain mean ($\bar{x}$) abundance and standard error (SE) by species. We estimated maximum abundance to better account for variation in annual energy demands. We included the species that comprised > 95% proportional abundance within the diving duck and shorebird guilds (Table 1).

We calculated the metabolic rate of individual species on the basis of a species' body mass, taxa-specific mass proportionality constant, and power exponent (Miller and Eadie 2006). We used body mass estimates from *The Birds of North America* Series (species, scientific names and citations in Table 1). We used body mass estimates from non-breeding or wintering populations where possible and, if data for males and females were available, we used the larger body mass estimate to avoid underestimating energy demand (Table 1).

For diving duck species, we calculated the Resting (or basal) Metabolic Rate (RMR) as RMR = 453 * $BM^{0.92}$ where BM= body mass (Miller and Eadie 2006). We then multiplied RMR by a conversion factor of three to estimate the Field Metabolic Rate (FMR; Heitmeyer 1989; Miller and Eadie 2006; Table 1). We obtained the values for all (except Western Sandpiper) shorebird species' mass proportionality constants and power exponents from Kersten and Piersma (1987) and estimated RMR = 437 * $BM^{0.729}$. We then converted RMR to field metabolic rate (FMR) by multiplying by three (Kersten and Piersma 1987). For Western Sandpipers, we used the direct estimate of the FMR from Tieleman and Williams (2000; Table 1). For all species, we estimated the Daily Energy Intake (DEI) – the amount of energy a bird consumes in kilojoule (kJ)/day/individual – from estimates of FMR divided by 0.73 to account for assimilation efficiency (Castro *et al.* 1989). We assumed no additional energy costs for weather or predator avoidance. We also assumed that birds were ideal foragers with equal ability to obtain food, and intake rate was limited by handling time and not prey density until prey were abruptly depleted (Goss-Custard *et al.* 2006).

To account for concurrent use of prey stocks across the winter season, we calculated use-days by species for each pond type. We did this by multiplying mean abundance by the number of days in the season from 1 December-28 February (90 days). We estimated the Total Energy Required ($T\hat{E}R$) for each guild across the study area (equation 1) as:

$$T\hat{E}R_g = \sum_{p=1}^{4}\sum_{s=1}^{i} DEI_s \cdot \hat{N}_{sp} \cdot d \qquad \text{(equation 1)}$$

where g = guild, p = pond type, s = species, DEI_s = Daily Energy Intake by species, $\hat{N}_{sp}$ = the abundance per species during the winter season by pond type, and d = the number of days in the season. We also estimated $T\hat{E}R$ separately by species and guild for each pond type, and for both average and maximum bird species' abundances, in order to estimate the avian energy requirements during both average and peak years.

Abundance and Energy Available from Benthic Invertebrates

We used a 3.5-m flat-bottom boat with a modified shallow-water outboard motor and standard Ekman grab sampler (15.2 cm × 15.2 cm × 15.2 cm) to sample benthic invertebrates in the interior of our study ponds. We collected samples from randomly selected grids per pond and then randomly selected cores per grid. During sampling events, we excluded grids within seasonal ponds with dry soil based on preliminary analyses that indicated dry areas lacked invertebrates.

We washed each grab sample in the field through a 1-mm mesh screen, preserved the remaining material in 70% ethyl alcohol and rose bengal dye, and then stored each in ethanol until processed. Invertebrates were sorted from debris, identified, and enumerated to

Table 1. Body mass and Field Metabolic Rates (FMR) of eight shorebird and four diving duck species from allometric equations based on species' body mass, mass proportionality constant, and power exponent. Daily Energy Intake (DEI) in units of kJ/day/individual by species.

Common Name	Scientific Name	Body Mass (kg)	FMR	DEI	Citation
Diving Ducks					
Ruddy Duck	*Oxyura jamaicensis*	0.598	846.81	1,160	Brua 2002
Canvasback	*Aythya valisineria*	1.368	1,812.48	2,483	Mowbray 2002
Lesser Scaup	*Aythya affinis*	0.721	1,005.82	1,378	Austin *et al.* 1998
Bufflehead	*Bucephala albeola*	0.465	671.86	920	Gauthier 1993
Shorebirds					
American Avocet	*Recurvirostra americana*	0.307	553.75	759	Robinson *et al.* 1997
Black-necked Stilt	*Himantopus mexicanus*	0.170	360.86	494	Robinson *et al.* 1999
Black-bellied Plover	*Pluvialis squatarola*	0.225	441.92	605	Dennis 1995
Marbled Godwit	*Limosa fedoa*	0.341	598.39	820	Gratto-Trevor 2000
Willet	*Catoptrophorus semipalmatus*	0.283	521.94	715	Lowther *et al.* 2001
Dunlin	*Calidris alpina*	0.058	164.70	226	Warnock and Gill 1996
Least Sandpiper	*Calidris minutilla*	0.021	78.16	107	Cooper 1994
Western Sandpiper	*Calidris mauri*	0.024	78.74	108	Wilson 1994

the lowest practical taxon (most to species or genus) and verified using taxonomic keys (Merritt and Cummins 1996; Carlton 2007) and expert confirmation.

Invertebrate samples were collected over a range of months and pond conditions from 2002-2007, from which we took a subset of the data to estimate average abundance of invertebrate taxa by pond type. We included samples collected October through March and estimated average salinities. We estimated average invertebrate abundances for the mesohaline circulation ponds from 234 grab samples in four ponds, and for the low-hyperhaline circulation ponds from 204 grab samples in four ponds at salinity levels equal to those when bird data were collected. Similarly, we estimated invertebrate abundances for low-hyperhaline seasonal ponds from 48 samples in three ponds and for medium-hyperhaline seasonal ponds from 96 samples in eight ponds. We estimated the average and standard error of abundance for each pond type.

To characterize biomass, we collected invertebrates in seven ponds from 2002-2004 that were sorted into 552 samples based on taxonomic group. We measured dry weight (DW) biomass of groups then divided by the number of individuals to obtain DW per individual.

Because assessment of available prey for shorebird and duck species from the literature generally occurred at a higher taxonomic level that that of our biomass samples (Table 2), we took a weighted average across biomass samples taken at the lower taxonomic levels used to estimate abundances of available prey. For the small number of taxa for which no biomass estimates were available from the South Bay Salt Ponds (Chironomidae, Diptera), we obtained biomass estimates from similar habitats (J. Y. Takekawa, unpubl. data).

We estimated energy content from primary prey for diving ducks and shorebirds (Brey *et al.* 1988). We converted energy content to Joules/g DW (Wacasey and Atkinson 1987) for Oligochaeta and Chironomidae (Gupta and Pant 1983), Artemia, Corixidae, and Ephydra (Caudell and Conover 2006), and Ostracod (Davis 1993). We obtained energy conversion for Hydrophilidae by averaging across similar taxa in Davis (1993). For the few taxa for which energy conversions were not available, we assumed energy content was similar to that of other taxa with similar taxonomy and biomass.

Estimating accessible habitat was a key component in calculating available energy. We estimated available habitat for diving ducks and shorebirds based on water depth ranges with ArcGIS (Environmental Systems Research Institute 2009). We collected monthly staff gage readings from 2007-2010 that were converted to water depth. To derive pond bottom elevations, we used bathymetry elevation data for 30 ponds (U.S. Geological Survey 2004) and LiDAR coverage for 13 ponds (Foxgrover and Jaffe 2005). We derived water depths by subtracting pond bottom elevations from the water surface elevation at a 25-m^2 pixel resolution. Depth values were set to zero when the ground surface elevation was higher than the water surface (i.e., the area was dry).

We assumed that diving ducks foraged in water depths between 0.5 and 2.5 m (Accurso 1992). Smaller shorebirds, such as Least and Western sandpipers, required depths greater than zero (i.e., not dry) and < 0.04 m, and larger shorebirds such as American Avocet and Black-necked Stilt foraged at depths < 0.18 m (Safran *et al.* 1997; Collazo *et al.* 2002). We assumed that there would be some variation in topography within 25-m^2 grid squares, and that at least one of the eight species of shorebirds within the guild could use the aggregate depth range. Thus, to avoid underestimating available habitat, we assumed that shorebirds foraged in grid cells with average water depths > 0 and ≤ 0.2 m.

We aggregated grid areas for 41 ponds to determine the average area of foraging habitat that was available or for 9% of the pond areas that were unknown, we applied the proportion of available habitat for each guild separately by pond. For five ponds in which water depth could not be determined, either due to missing pond

Table 2. Average abundance ± SE of invertebrate prey taxon per grab sample for diving ducks (D) and shorebirds (S) in four pond types. Aggregate prey taxa by guild wereidentified from the literature cited in Table 1.

Invertebrate Taxa	Prey	Circulation Ponds		Seasonal Ponds	
		Mesohaline	Low-hyperhaline	Low-hyperhaline	Medium-hyperhaline
Oligochaeta	S/D	63.89 ± 9.95	15.51 ± 3.30	0	0
Polychaeta	S/D	224.00 ± 22.94	90.85 ± 14.81	0.04 ± 0.04	0
Ostracoda	S/D	11.26 ± 5.17	0.33 ± 0.16	0.29 ± 0.29	0
Artemiidae	S	0	2.83 ± 0.57	2.00 ± 0.74	56.38 ± 9.55
Amphipoda	S/D	233.60 ± 39.8	132.11 ± 25.30	0	0
Cumacea	S	0.13 ± 0.05	0.51 ± 0.20	0	0
Isopoda	S/D	0.32 ± 0.14	0.19 ± 0.06	0	0
Hydrophilidae	S	0.01 ± 0.01	0.26 ± 0.08	0	0.13 ± 0.05
Ephydridae	S/D	0.01 ± 0.01	0	1.13 ± 0.35	29.90 ± 13.73
Chironomidae	S/D	18.88 ± 6.23	0	0	0
Other Diptera	S/D	0.08 ± 0.04	0.03 ± 0.02	0.92 ± 0.30	2.59 ± 0.59
Corixidae	S/D	0.03 ± 0.02	0.73 ± 0.37	0.77 ± 0.40	0.82 ± 0.20
Bivalvia	S/D	4.49 ± 1.12	2.30 ± 0.80	0	0
Gastropoda	S/D	10.24 ± 3.22	0.17 ± 0.05	0	0
Nemertea	S	3.66 ± 0.94	0.52 ± 0.20	0	0

bottom or water surface elevation data, we applied the proportion of available habitat of ponds of the same type. We then summed to determine the foraging area (ha; $\bar{x}$ ± SE) available for diving ducks and shorebirds with XTools Pro Aggregate Features/Records in ArcGIS.

We estimated Energy Density (ED; in joules/m^2) and Total Energy Available ($T\hat{E}A$; in joules) on the basis of invertebrate abundance by invertebrate taxon and pond type ($\hat{N}_{tp}$), biomass by taxon ($\hat{B}_t$), energy by taxon ($\hat{E}_t$), available habitat by guild and pond type ($\hat{A}_{gp}$), and a multiplier to convert to unit area. We estimated ED for each guild and pond type (equation 2), and Total Energy Available ($T\hat{E}A$) by guild within and across pond types (equation 3) as:

$$\hat{ED}_{gp} = \sum_{t=1}^{i} \hat{N}_{tp} \cdot \hat{B}_t \cdot E_t \cdot c \qquad \text{(equation 2)}$$

$$T\hat{E}A_g = \sum_{p=1}^{4} \hat{A}_{gp} \sum_{t=1}^{i} \hat{N}_{tp} \cdot \hat{B}_t \cdot \hat{E}_t \cdot c \qquad \text{(equation 3)}$$

where g specifies the primary prey by avian guild, p = pond type, t = invertebrate taxon, and c is a multiplier to aggregate from the sampled area to square meters. To measure the uncertainty associated with the $T\hat{E}A$, we used the delta method (Powell 2007) to estimate standard errors that incorporated the uncertainty associated with invertebrate abundance and biomass. Invertebrate abundance and biomass estimates were derived from different samples and thus were independent. We incorporated covariances among invertebrate abundance estimates within pond types since these were obtained from the same grab samples, and used covariances pertaining to taxon-specific invertebrate abundances by pond type within the variance-covariance matrix for the delta method. We interpreted meaningful differences in terms of non-overlapping 95% confidence intervals.

Carrying Capacity for Diving Ducks and Shorebirds

We compared $T\hat{E}R$ vs. $T\hat{E}A$ to assess energy requirements for each guild at both average and maximum abundances. We then estimated shorebird and diving duck use-days with a daily ration model in which we defined carrying capacity as the potential number of use-days the managed ponds can support over the winter on the basis of available prey energy (Goss-Custard *et al.* 2002, 2003). We estimated use-days by dividing $T\hat{E}A$ of consumable food by the DEI weighted by species or guild consumption at average abundance.

We adjusted by area to estimate potential use-days·ha^{-1} in two ways. First, we estimated use-days·ha^{-1} of total area in each pond type, which provided an estimate of use-days that can be supported given observed water depths. For comparison, we also estimated use-days·ha^{-1} of available habitat (i.e., assuming all areas had appropriate water depths for each guild) by pond type, which provided an estimate of the potential maximum number of use-days that could be supported if pond bathymetries were changed, assuming no density-dependent effects.

RESULTS

Avian Abundances and Energy Requirements

We estimated 35,450 ± 1,559 ($\bar{x}$ ± SE) diving ducks in average years and 45,458 ± 1,653 ($\bar{x}$ ± SE) in peak years during winters 2007-2010. During average and peak years, diving ducks were composed of Ruddy Duck (61-64%), Lesser Scaup (25-27%), Canvasback (5-7%), and Bufflehead (6%; Fig. 2). At least 95% of individual diving ducks were detected in circulation ponds in both average and peak years. Of these diving ducks in circulation ponds, abundances were three to four times greater in mesohaline than low-hyperhaline ponds (Fig. 2).

We estimated 64,253 ± 14,838 ($\bar{x}$ ± SE) shorebirds in average years and 108,171 ± 4,854 ($\bar{x}$ ± SE) in peak years. Shorebirds were composed of Western Sandpiper (44%), Dunlin (24-27%), Black-bellied Plover (9-10%), American Avocet (7-8%), Least Sandpiper (4-6%), Willet (3%), Marbled Godwit (2-4%), and Black-necked Stilt (2%; Fig. 2). An average of 69% and 64% of shorebirds were detected in seasonal ponds in average and peak years, respectively, both with greater abundances in low-hyperhaline compared with medium-hyperhaline ponds (Fig. 2).

The DEI for diving ducks ranged from 920 kJ/individual/day for Bufflehead to 2,483 kJ/individual/day for Canvasback (Table 1). The $T\hat{E}R$ for average abundance over the winter season was greater in circulation ponds than in seasonal ponds, and greater in mesohaline vs. low-hyperhaline circulation ponds for all species and the guild as a whole, which mimicked observed abundance patterns (Fig. 2). The $T\hat{E}R$ for maximum abundances was 29% greater overall, but relative energy required across pond types were similar to those of average abundances (Fig. 2).

Energy requirements for shorebirds also varied among species and pond types over the winter season. The DEI ranged from 107

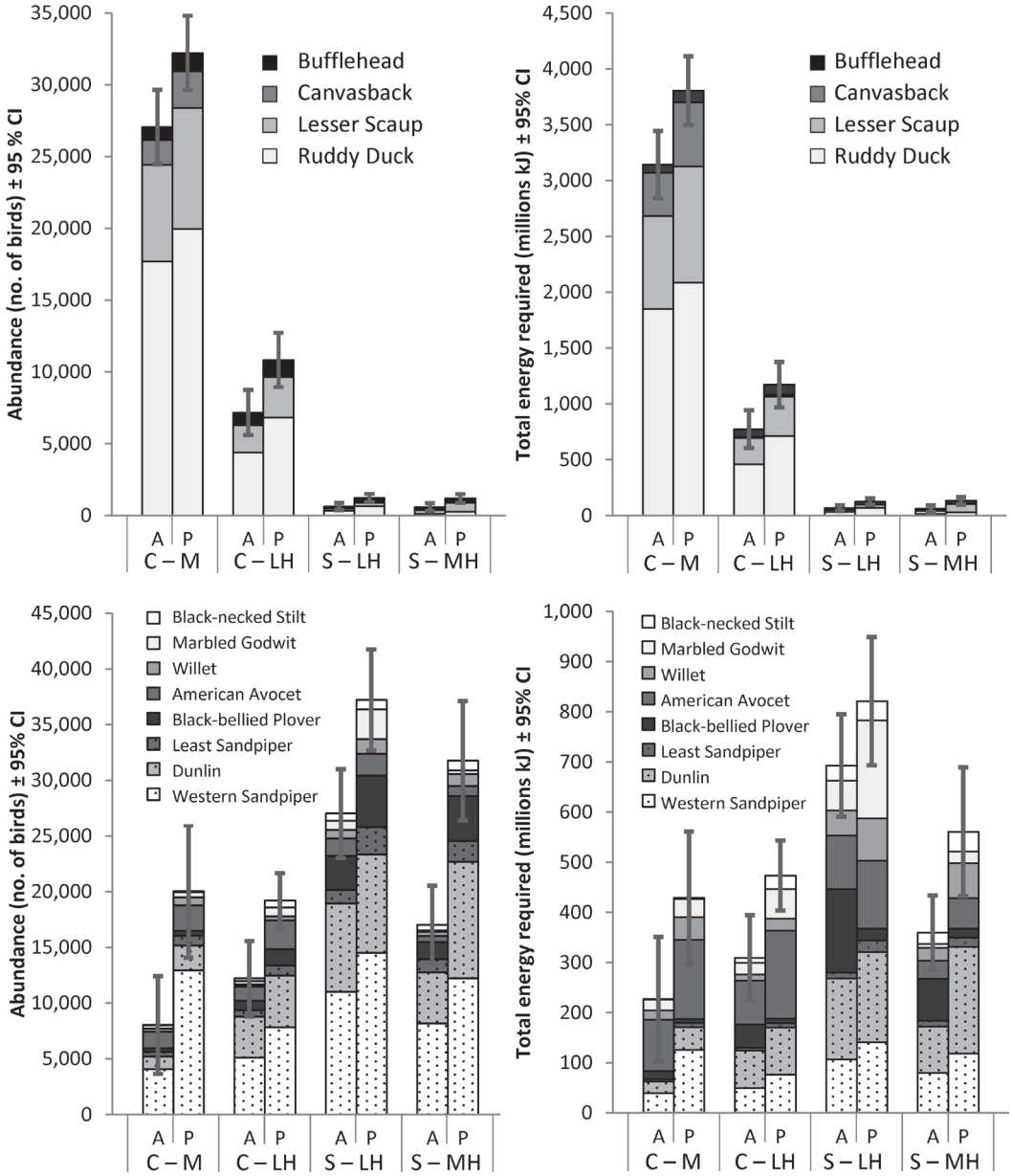

Figure 2. Species' abundances (left) and total energy required (right) at average (A) and peak (P) years with 95% CI for four diving duck species (top) and eight shorebird species (bottom) in four pond types: Circulation – mesohaline (C – M), Circulation – low-hyperhaline (C – LH), Seasonal – low-hyperhaline (S – LH), and Seasonal – medium-hyperhaline (S – MH). CIs pertain to total abundances and energy intake across species within each guild by pond type.

kJ/individual/day for Least Sandpiper to 820 kJ/individual/day for Marbled Godwit (Table 1). At average abundance levels, the $\hat{TER}$ was greater in seasonal ponds than in circulation ponds, and generally greater in low-hyperhaline seasonal ponds compared with medium-hyperhaline seasonal ponds (Fig. 2). The relative energy requirements varied as a function of both abundance and among-species DEI, which reflected substantial differences in body mass. Across the study area, Western Sandpiper, Dunlin, Black-bellied Plover, and

American Avocet had the greatest overall energy requirements, reflecting high abundances or body mass. The *TÊR* for maximum abundances was 79% greater overall than at average abundances levels, but otherwise energy required across pond types were similar to those of average abundances (Fig. 2).

Abundance and Energy Available from Benthic Invertebrates

Among 15 benthic invertebrate taxa, there were substantial differences in average abundance per sample among pond types. Three taxa had greatest density in seasonal ponds, all of which had significantly higher density in medium- than low-hyperhaline ponds (Table 2). Of eight taxa with greatest abundance in circulation ponds, all had substantially greater abundances in mesohaline ponds than in low-hyperhaline ponds, most with non-overlapping confidence intervals (Table 2).

The ED incorporated invertebrate taxa abundance, biomass, and energy content. For both diving ducks and shorebirds in mesohaline circulation ponds, the majority of ED was provided by polychaetes (58-63%), bivalves (25-29%), and amphipods (8-10%), with less than 3% each for all other taxa (Fig. 3). Low-hyperhaline circulation ponds had similar taxonomic composition, but ED was less than half that of mesohaline circulation ponds with non-overlapping confidence intervals (Fig. 3). The ED was substantially lower in seasonal ponds than circulation ponds for diving ducks and shorebirds. Within seasonal ponds, ED was greater in medium-hyperhaline ponds compared with low-hyperhaline ponds for both guilds (Fig. 3).

The area of accessible habitat varied by pond type for both guilds. Of the 1,803 ha of mesohaline circulation ponds, we estimated 55 ± 8% ($\bar{x}$ ± SE) were available to diving ducks and 11 ± 3% were available to shorebirds over the study period. Of 1,288 ha of low-hyperhaline circulation ponds, 68 ± 8% were available to diving ducks and only 2 ± 1% were available to shorebirds. A greater percentage of seasonal ponds was available to shorebirds. Of the 677 ha of low-hyperhaline seasonal ponds, 40 ± 6% was available to shorebirds and 13 ± 3% to diving ducks. Of the 975 ha of medium-hyperhaline seasonal ponds, 36 ± 9% was available to shorebirds and 22 ± 9% was available to diving ducks.

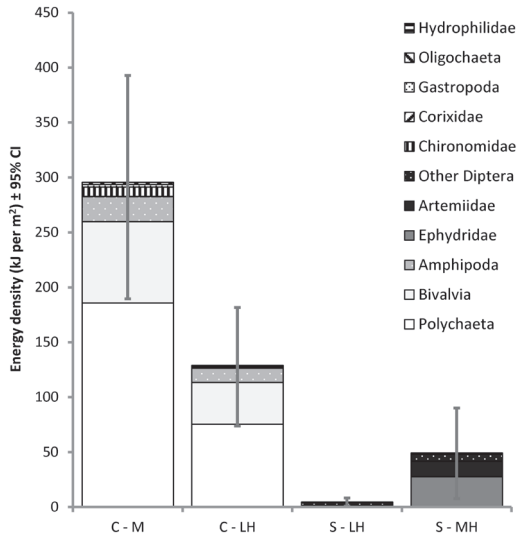

Figure 3. Energy density (ED) with 95% confidence intervals (CI) from invertebrate taxa in four pond types: Circulation – mesohaline (C – M), Circulation – low-hyperhaline (C – LH), Seasonal – low-hyperhaline (S – LH), and Seasonal – medium-hyperhaline (S – MH). Invertebrate taxa (Nemertea, Ostracoda, Isopoda, Cumacea) comprising ≤ 1% of the total were excluded. CIs pertain to total energy density across taxa by pond type.

The *TÊA* differed substantially between diving ducks and shorebirds across pond types and was low for both diving ducks and shorebirds in seasonal ponds (Fig. 4). *TÊA* was substantially lower for shorebirds than diving ducks in circulation ponds, largely reflecting the small area of accessible habitat. For shorebirds, *TÊA* was 18 times greater in mesohaline circulation ponds than low-hyperhaline circulation ponds, reflecting both lower ED and lower available habitat. However, despite a smaller area of accessible habitat for shorebirds, *TÊA* for shorebirds in mesohaline circulation ponds was 49 times greater than in low-hyperhaline seasonal ponds and was 3.5 times greater than in medium-hyperhaline seasonal ponds (Fig. 4).

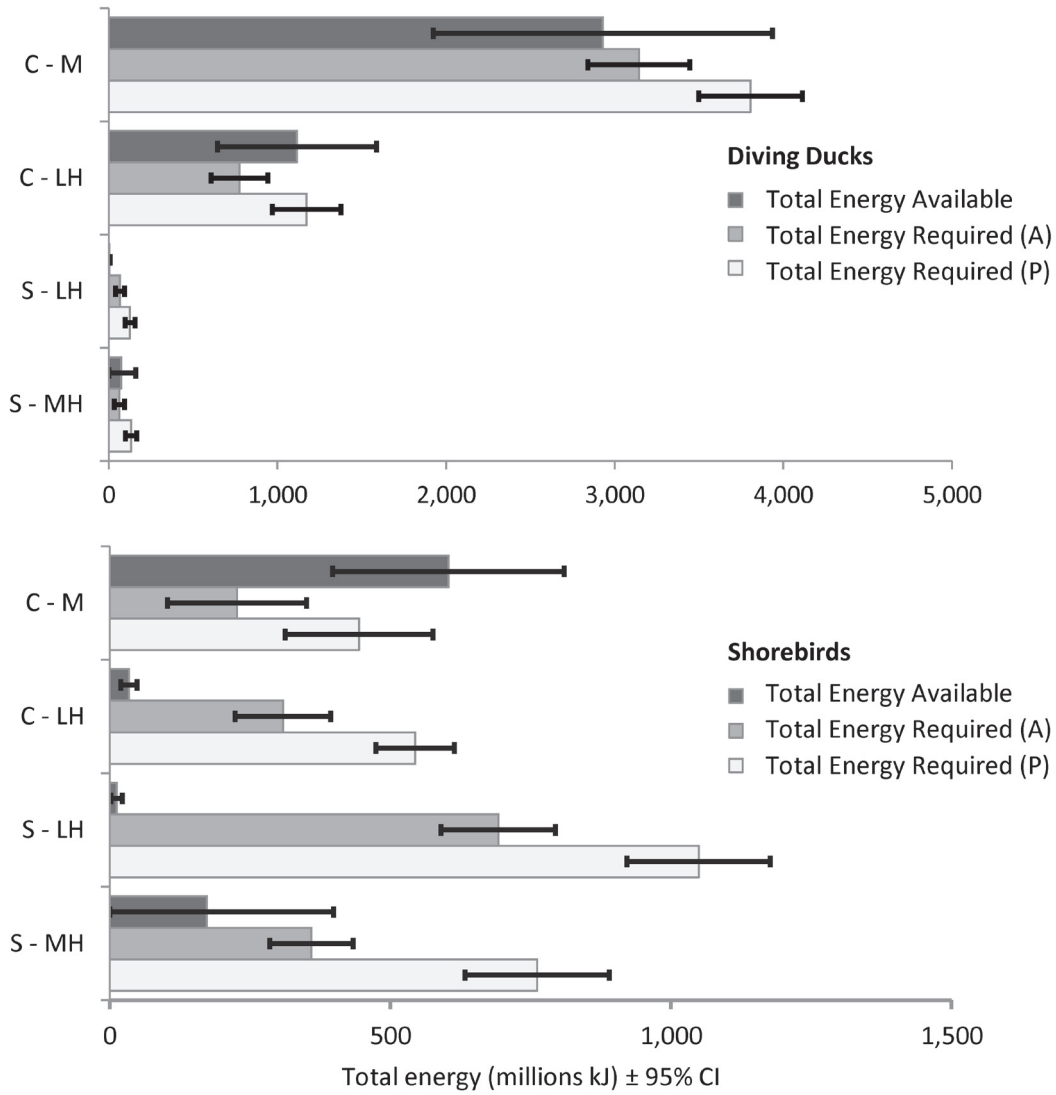

Figure 4. Total energy available (dark gray) and total energy required at average (A; medium gray) and peak (P; light gray) years for diving ducks (top) and shorebirds (bottom) in each pond by type in millions kJ ± 95% confidence interval (CI). Pond types: Circulation – mesohaline (C – M), Circulation – low-hyperhaline (C – LH), Seasonal – low-hyperhaline (S – LH), and Seasonal – medium-hyperhaline (S – MH).

Carrying Capacity for Diving Ducks and Shorebirds

We compared *TÊR* with *TÊA* by guild in different pond types (Fig. 4). We found that the energy intake needed by diving ducks in mesohaline circulation ponds was largely supported by available prey, with 93% provided at average abundances and 77% at maximum abundances with overlapping confidence intervals. The lower energy required by diving ducks in low-hyperhaline circulation ponds was also supported by available energy at average abundances (Fig. 4). Energy intake and energy available in seasonal ponds was extremely low for diving ducks.

Available energy was less than required for shorebirds in three of four pond types. *TÊA* for shorebirds in low-hyperhaline seasonal ponds was only 1-2% of that required at average and maximum abundances. In medium-hyperha-

line ponds, *TÊA* was 48% of the energy intake required to maintain average abundances and 23% of the energy intake required to maintain maximum abundances. Available energy was also less than that required for shorebirds in low-hyperhaline circulation ponds. In contrast, mesohaline circulation ponds maintained 266% of that required for average abundances and 136% of that required for maximum abundances (Fig. 4).

Overall, the South Bay Salt Ponds provided greater energy for diving ducks than shorebirds. The study area provided 102% of energy needs for diving ducks at average abundance and 79% at maximum abundance (Fig. 5). For shorebirds, the study area provided 52% of energy needs at average abundance and 29% at maximum abundance (Fig. 5).

Potential use-days·ha^{-1} of available habitat was substantially higher in mesohaline circulation ponds than any other pond type for both diving ducks and shorebirds (Fig. 6). Low-hyperhaline circulation ponds had the second greatest potential use-days·ha^{-1} of available habitat, followed by medium-hyperhaline seasonal ponds. However, use-days·ha^{-1} of available habitat was highly variable in medium-hyperhaline ponds for both diving ducks and shorebirds with non-overlapping confidence intervals. Bird use-days·ha^{-1} of the total area was substantially lower than available habitat for diving ducks and shorebirds in every pond type (Fig. 6).

DISCUSSION

Over 90% of California's two million hectares of historic wetlands have been lost, and remaining stopover and wintering sites are limited to a patchwork of public and privately owned lands that now must fill the role of historic wetlands (Shuford *et al.* 1998; Stralberg *et al.* 2011). We found that supratidal foraging habitat in South San Francisco Bay provides an important supplement for energy required for waterbirds, similar to findings in other coastal estuaries (Velasquez and Hockey 1992; Weber and Haig 1996; Masero and Pérez-Hurtado 2001). The relatively high energy available across the study area for diving ducks (79 and 102% of that required at maximum and average abundances, respectively) suggests that diving ducks use managed ponds not only as roosting habitat but also as important foraging areas. The available energy was lower for shorebirds but still represented 52% of their need at average abundances and 29% at maximum abundances. Similarly, Masero and Pérez-Hurtado (2001) found that salt works adjacent to natural mudflats in southern Spain provided 23-82% of energy required for Redshank (*Tringa tetanus*). Velasquez and Hockey (1992) suggested that supratidal habitats in the Berg estuary of South Africa supported 17-100% of energy requirements for different wading species

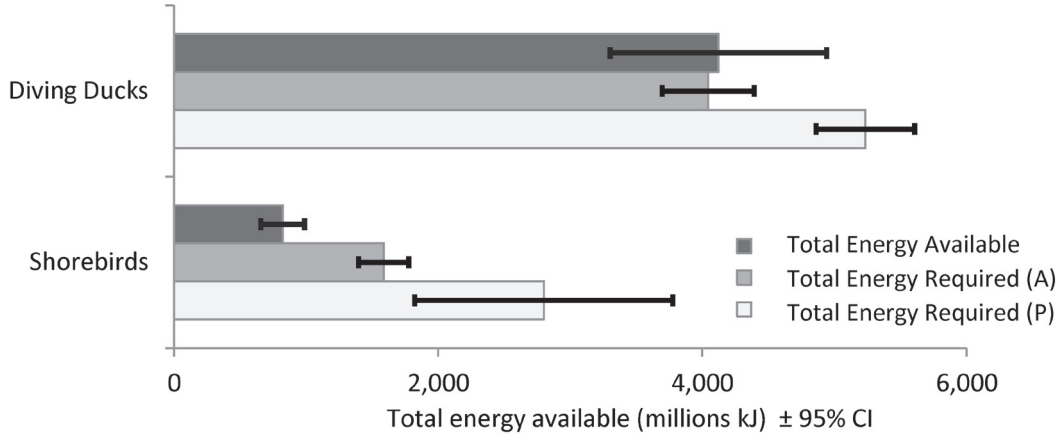

Figure 5. Total energy available (dark gray) and total energy required at average (A; medium gray) and peak (P; light gray) years for diving ducks and shorebirds in all ponds within the study area in millions kJ ± 95% confidence interval (CI).

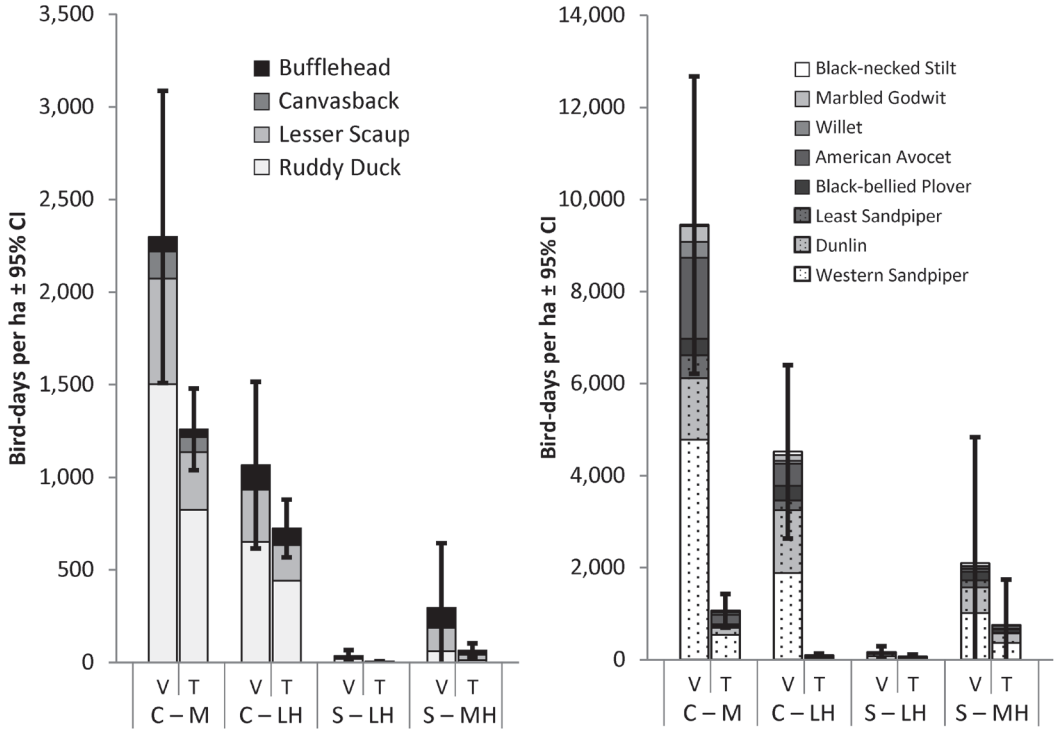

Figure 6. Bird-days per ha of available habitat (V) and per ha of total area (T) by pond type for diving ducks (left) and shorebirds (right) ± 95% confidence interval (CI). Pond types: Circulation – mesohaline (C – M), Circulation – low-hyperhaline (C – LH), Seasonal – low-hyperhaline (S – LH), and Seasonal – medium-hyperhaline (S – MH). CIs pertain to bird-days per ha across species within each guild and pond type.

compared with adjacent mudflats. However, avian use of supratidal habitats differed markedly on the basis of salinity and water depth in Guadiana estuary, Portugal (Dias 2009), similar to our findings.

Circulation ponds supported > 95% of diving duck abundance, but we found substantially greater bird abundances, invertebrate abundances, and energy density in mesohaline circulation ponds than in low-hyperhaline circulation ponds. Other studies have documented greater invertebrate abundances in lower salinity conditions, with loss of certain invertebrates such as chironomids and amphipods above 30-40 ppt thresholds (Velasquez and Hockey 1992; Andrei *et al.* 2008). Some studies have documented selective diets for diving ducks, such as amphipods for Lesser Scaup (Anteau and Afton 2009); however, Takekawa *et al.* (2009) documented dietary flexibility in Ruddy Duck, which selected amphipods and bivalves in a low salinity pond (22 ppt), but in a higher salinity pond (40 ppt) selected *Polydora*, a common polychaete species that also dominated our samples. Euliss *et al.* (1991) documented that Ruddy Ducks were opportunistic foragers in inland evaporation ponds, shifting their diets to the most abundant prey types. It is unknown the degree to which the other common diving duck species exhibit dietary flexibility in our system; however, all have shown substantial variation in diet among other studies (Gauthier 1993; Austin *et al.* 1998; Brua 2002; Mowbray 2002). Generally, we found that diving duck energy requirements were similar to energy available, suggesting that they distribute according to prey availability, which was highest in mesohaline circulation ponds.

In contrast to diving ducks, shorebirds were most abundant in seasonal ponds, with more in low- than medium-hyperhaline ponds. However, we found that energy den-

sity of invertebrates was extremely limited in low-hyperhaline seasonal ponds, providing only 1-2% of that required. Compared with circulation ponds with similar salinity ranges, the lower invertebrate biomass in seasonal ponds may have resulted from hydrologic closure that limited colonization of aquatic invertebrates (Ruhi *et al.* 2009). The low energy available in the low-hyperhaline seasonal pond type suggests that large numbers of shorebirds (e.g., > 37,000 birds in peak years) primarily used these ponds to roost. Roosting sites preferred by shorebirds are large to reduce disturbance or predation risk, are close to feeding areas to minimize energetic costs, and provide shelter from prevailing winds (Burton *et al.* 1996; Colwell *et al.* 2003; Dias 2009; Sripanomyom *et al.* 2011). However, shorebirds may minimize use of roosts when alternative foraging habitats are available during high tide (Colwell *et al.* 2003).

Medium-hyperhaline ponds had significantly greater abundances and energy density of invertebrates relative to low-hyperhaline seasonal ponds; these invertebrates were mostly composed of Artemiidae (brine shrimp) and Ephydridae (brine fly) larvae. Other studies have documented greatest abundances of these taxa in salinities > 80 ppt (Herbst 2006; Takekawa *et al.* 2006). While Artemiidae was considered a minor diet component, Ephydridae and other Diptera larvae were selected by Western Sandpiper and American Avocet and likely comprise a major portion their diets in medium-hyperhaline ponds (Herbst 2006; Takekawa *et al.* 2009). We observed a high degree of variation in Ephydridae abundances in higher salinity seasonal ponds, but additional work is needed to assess sources of this variation that could occur among ponds, within ponds, or over time, to better enable management of this prey resource in hyperhaline conditions.

Despite greater abundances in seasonal ponds, we found that the total energy available for shorebirds and the number of bird use-days·ha^{-1} of available habitat was greater in mesohaline circulation ponds than any other pond type. Other studies that had a wide range of salinity conditions documented either greater shorebird or invertebrate abundance with salinity levels < 30-40 ppt (Velasquez 1992; Andrei *et al.* 2008; Dias 2009), although a smaller number of species specialized in higher salinity conditions (Velasquez and Hockey 1992; Dias 2009). Andrei *et al.* (2008) documented that freshwater inputs in saline lakes extended hydroperiods and decreased salinity levels to allow development of aquatic invertebrate prey for shorebirds. Increased hydrological connectivity with inflows of freshwater from adjoining uplands or riparian areas may be beneficial in the South Bay as well. Pond types with mesohaline conditions maintained the greatest densities of invertebrates, and this was the only pond type in which energy available for shorebirds exceeded their requirements. While we were unable to consider prey size explicitly in this study, our samples were primarily composed of *Gemma gemma* (bivalve), *Polydora* spp., and *Capitella* spp. (polychaetes) that along with amphipods are likely prey for small to larger shorebirds (Quammen 1982; Safran *et al.* 1997; Takekawa *et al.* 2009). Further work is needed to better understand factors that could have altered habitat selection by foraging shorebirds, such as sediment texture (Quammen 1982), landscape position (Taft and Haig 2006), temporally dynamic island exposure (Colwell *et al.* 2003), prey predictability (Kraan *et al.* 2009), or prey selection (Takekawa *et al.* 2009). Also, some species of shorebirds, especially Western Sandpiper, may consume biofilm as part of their diets (Kuwae *et al.* 2012), but abundance and importance of this resource to shorebirds in managed ponds is unknown.

Water depth strongly influences habitat availability for particular species of waterbirds (Velasquez 1992; Safran *et al.* 1997; Taft *et al.* 2002; Dias 2009). Rapid, dramatic changes in shorebird use have occurred with changes in water depths in diked wetlands (Velasquez 1992; Collazo *et al.* 2002; Taft *et al.* 2002). We found that bird use-days could be enhanced by increasing the area available at preferred water depths. Since water depths of available habitat for diving ducks

and shorebirds are mutually exclusive, multi-species pond management would require control of water levels among ponds and alteration of bathymetry to optimize foraging depths for diverse bird groups. Future studies could project waterbird responses to management scenarios that alter salinity and accessible habitat to evaluate potential foraging habitat in managed ponds or mitigate for loss of mudflats. With potential reduction in foraging habitat, however, future research should evaluate density dependent effects because foraging in high density flocks may increase interference competition or deplete prey (Santos *et al.* 2005; Goss-Custard *et al.* 2006; Dias 2009).

San Francisco Bay supports abundant populations of non-breeding, migratory waterbirds, and we have shown how different types of managed ponds affect foraging resources for diving ducks and shorebirds in the South Bay. The effort to minimize loss of foraging resources for waterbirds remains critical, following empirical evidence of declines in body condition, survivorship, and population sizes of waterbirds with reduction in the extent or quality of foraging resources at landscape scales (Burton *et al.* 2006; Kraan *et al.* 2009). In addition to the importance of foraging resources for diving ducks and shorebirds during the winter, Masero and Pérez-Hurtado (2001) found a fourfold increase in energy intake in supratidal vs. mudflat habitats during migration compared with the winter for Redshank (*Tringa tetanus*) in southern Spain. We suggest that wetland management be targeted for winter and migration periods when waterbirds likely experience the greatest energy demands (Velasquez and Hockey 1992; Skagen and Knopf 1993; Shuford *et al.* 1998).

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