Kelly, J. P., J. G. Evens, R. W. Stallcup, and D. Wimpfheimer. 1996.
The effects of aquaculture on habitat use by wintering shorebirds.
California Fish and Game 82(4): 160-174.

EFFECTS OF AQUACULTURE ON HABITAT USE BY WINTERING SHOREBIRDS IN TOMALES BAY, CALIFORNIA

JOHN P. KELLY, JULES G. EVENS, RICHARD W. STALLCUP, and DAVID WIMPFHEIMER

Audubon Canyon Ranch
Cypress Grove Preserve
P.O. Box 808
Marshall, California 94940

We measured abundances of wintering shorebird species simultaneously on four control plots and two aquaculture plots from November 1989 to February 1994 on tidal flats in Tomales Bay, California. Twelve abundance estimates for each plot were obtained each year. We used analysis of covariance to model the results, controlling for the presence of roosting gulls that may have displaced foraging shorebirds. The analysis included effects related to intraseasonal timing, annual variation, and the presence of aquaculture. The two most abundant shorebird species in Tomales Bay, western sandpiper, *Calidris mauri*, and dunlin, *Calidris alpina*, significantly avoided aquaculture areas. Willets, *Catoptrophorus semipalmatus*, however, were attracted to aquaculture plots. Four other species showed no preferences for control or aquaculture plots. Evidence of underlying (pre-existing) habitat conditions did not explain these results. We found no differences in species richness or Shannon diversity index between control and aquaculture areas. Our results suggest a net decrease in total shorebird use in areas developed for aquaculture .

INTRODUCTION

Shorebird populations generally concentrate where feeding efficiency is greatest (Goss-Custard 1970, Connors et al. 1981; reviews by Evans and Dugan 1984, Meire and Kuyken 1984, and Puttick 1984) and invertebrate prey density (Goss-Custard et al. 1977, Bryant 1979, Wilson 1990, Colwell and Landrum 1993) or availability (Recher 1966, Myers et al. 1980, Goss-Custard 1984) is highest. Sediment characteristics can influence shorebird distribution and density by affecting prey density or availability (Page et al. 1979, Quammen 1982, Yates et al. 1993). Foraging distributions and densities of shorebirds are also influenced by other macrohabitat (Burger 1984a) and microhabitat characteristics (Recher 1966, Baker and Baker 1973, Gerstenberg 1979, Burger 1984b). In some species, social behavior determines the extent to which habitat characteristics or food availability influence numbers of shorebirds using a particular area (Myers 1984).

Pacific oyster, *Crassostrea gigas*, culture alters spatial habitat structure by introducing shellfish, racks, stakes, culture bags, marker poles, and other equipment onto open tidal flats. Research conducted to date on ecosystem effects of oyster culture has been limited to studies of effects on sediment (Ottmann and Sornin 1985, Deslous-Paoli et al. 1992) and benthic infauna (Triani[1] 1994); effects of oyster culture on bird populations have not been addressed. Therefore, from 1989 to 1994, we investigated the use of intertidal mud flats by wintering shorebirds in relation to Pacific oyster growing operations at Walker Creek Delta, Tomales Bay, California. Study objectives were to (i) test for selection or avoidance of aquaculture areas by wintering shorebirds, (ii) test for differences in shorebird diversity between open tidal flats and aquaculture areas, (iii) examine temporal and spatial variation of shorebird abundance on open tidal flats and aquaculture areas, and (iv) compare intraseasonal shifts in use of tidal flats and aquaculture areas with overall abundance changes in Tomales Bay.

STUDY AREA AND METHODS

We conducted the study on test plots at Walker Creek Delta near the north end of Tomales Bay, California (Figure 1). Tidal flats on the delta were composed of consolidated fine sands, silts, and clays

(Daetwyler 1966) and were divided by three creek channels. We marked six study plots around the perimeter of the delta, each plot occupying 225 meters of shoreline and covering approximately 2.0 ha of tidal flat between 0.0 and 0.3 m above mean lower low water (MLLW; Fig. 1). Two control plots (Plots 1 and 2) were on the south perimeter of the delta. Two others (Plots 3 and 4) were designated as treatment plots on currently used aquaculture lease areas (Fig. 1). We established Plots 5 and 6 on undeveloped aquaculture areas to provide temporal experimental control as they were developed for aquaculture; however, aquaculture development did not occur as expected. Instead, local oyster growers developed an area that included approximately 15% of Plot 6 by the end of the 1992-93 sampling period (Fig. 1). This aquaculture operation was abandoned subsequently and the aquaculture equipment was removed prior to the 1993-94 sampling period. Control and aquaculture test areas were separated by at least 100 m; within control and aquaculture areas, plots were separated by 50 m.

Oyster growers used 0.61 x 0.91-m black plastic mesh bags placed on the bottom and 0.30 to 0.61 m above the bottom on 1.22 x 2.44-m steel re-bar frames supported by PVC pipe legs. The ends of rows of oyster bags were often marked with 1- to 2.5-meter-high PVC stakes.

We conducted three counts per month on each plot, from November through February 1989-90 to 1993-94. Count days were clustered in groups of three, usually consecutive days during spring tides. Three observers, each observing two plots, used telescopes to conduct simultaneous counts of all shorebirds on the six study plots. Observers rotated among pairs of plots on successive days. Each count period consisted of three 20-min counts initiated at 30-min intervals as the edge of the falling tide receded through the study plots; shorebirds generally foraged near the edge of the falling tide (Recher 1966, Evans and Dugan 1984). We recorded the peak number of birds of each species seen in each plot during each 20-min. count interval. Abundances from the three count intervals were averaged to provide an index of shorebird use. We did not estimate absolute density because of increasing exposure of suitable foraging habitat as the water level receded.

To account for possible population effects on annual and intraseasonal differences in habitat use, we compared results with Tomales Bay-wide counts (Kelly[2] 1990-94). We conducted three Tomales Bay-wide counts in early winter (November-December) and three in late winter (15 January - 28 February)

each year. We generally scheduled Tomales Bay-wide counts within 3-7 days of plot counts. Kelly[3] (1990) described the census methods.

Statistical Analysis

We used a mixed-model analysis of covariance (ANCOVA), controlling for displacement of shorebirds by roosting gulls, to model patterns of abundance. Prior to the analysis, the plot counts were log-transformed to normalize the data. Aquaculture treatment (presence or absence) and intraseasonal timing (early vs. late winter) were considered to be fixed effects; plots (nested within control and aquaculture areas) and years were considered to be random effects. We used this same analysis method to examine species diversity within plot counts, based on the Shannon index (Magurran 1988: 36). We tested for associations between the abundance of gulls and shorebirds on the study plots using correlation analysis.

We investigated the possibility that habitat use gradients occur on the delta by using ANCOVA to test for differences (fixed effects) between (i) control plots on the northwest (Plots 5 and 6) and southeast (Plots 1 and 2) sides of the delta and (ii) control plots on the inner (Plots 1 and 6) and outer (Plots 2 and 5) portions of the delta (Fig. 1). We examined the possible influence of the partial use of Plot 6 for aquaculture on shorebird abundances by using ANCOVA to test for differences (fixed effects) between (i) Plot 6 in 1992-93 and the other 4 years of study, and (ii) Plot 6 and the other control plots in 1992-93. Further, ANCOVA models generated for each species were repeated after removing the 1992-93 Plot 6 data, and examined for differences in the significance levels of individual effects.

A maximum likelihood approach was used to estimate the parameters of the ANCOVA models (BMDP Program 3V, Dixon 1992). The significance of each source of variation was tested with a likelihood ratio chi-square comparing the original model with a submodel in which the associated parameter was set to zero.

RESULTS

While completing 360 shorebird plot counts, we observed dense concentrations of gulls roosting on Walker Creek Delta. The maximum number of gulls observed within a plot was 7400; the median was 65. Of all gulls observed on study plots, 76.6% were California gulls, *Larus californicus*; 18.2% were western, *Larus occidentalis*, or glaucous-winged gulls , *Larus glaucescens*; 5.4% were ring-billed gulls, *Larus delawarensis*; and 0.8% were mew gulls, *Larus canus*. The number of gulls occupying study plots was inversely related to the number of marbled godwits, *Limosa fedoa* ($r = -0.15$, $P < 0.001$); western sandpipers, *Calidris mauri* ($r = -0.20$, $P < 0.001$); least sandpipers, *Calidris minutilla (*$r = -0.21$, $P <$); dunlins, *Calidris alpina* ($r = -0.26$, $P < 0.001$); willets, *Catoptrophorus semipalmatus* ($r = -0.12$, $p < 0.05$); and all shorebirds combined ($r = -.25$, $P < 0.001$). Correlations of gull abundance with black-bellied plover, *Pluvialis squatarola (*$r = -0.08$), and sanderling, *Calidris alba* ($r = -0.04$), numbers were negative but not significant ($P > 0.05$).

It is not likely that these relationships resulted from differences in habitat use because gulls and shorebirds used the same areas and we obtained similar results in separate within-plot analyses. The negative signs of correlation coefficients between gulls and all seven species of shorebirds analyzed in this paper suggest that roosting gulls displaced shorebirds in areas of otherwise suitable shorebird habitat. Therefore, we used ANCOVA to control for the effects of roosting gulls on the use of control and aquaculture plots by shorebirds.

Oyster workers were present on aquaculture areas during 62% of our counts, suggesting that human activity might have influenced bird distributions. However, the distribution of gulls on the delta was not related to the presence of oyster workers (likelihood ratio = 0.58, $P > 0.45$) or developed aquaculture areas (likelihood ratio = 0.001, $P > 0.97$). We observed no movements of shorebirds into or out of plots in response to human activity and the distributions of shorebirds were not significantly related to the presence of oyster workers on aquaculture plots (ANCOVA; P = 0.11, 0.59, 0.89, 0.10, 0.49, 0.68, 0.17, for black-bellied plover, willet, marbled godwit, sanderling, western sandpiper, least sandpiper, and dunlin, respectively).

The most abundant shorebird species we observed was dunlin, followed by least sandpiper and western sandpiper (Table 1). Sanderlings and larger shorebirds such as marbled godwits and willets were less abundant. Greater yellowlegs, *Tringa melanoleuca*, ruddy turnstones, *Arenaria interpres*, black turnstones, *Arenaria melanocephala*, short-billed dowitchers, *Limnodromus griseus*, and long-billed dowitchers, *Limnodromus scolopaceus*, each occurred on less than 10% of plot counts.

Data for seven species were adequate for parametric tests of the hypothesis that abundance on aquaculture and control areas did not differ (Table 2). Differences between the use of control and aquaculture areas by black-bellied plovers, marbled godwits, sanderlings, and least sandpipers were not significantly different than expected by chance, given the underlying variation among the nested plots (Tables 1 and 2). However, western sandpipers and dunlins were significantly less abundant and willets significantly more abundant on aquaculture plots than on control plots.

A significant difference in the use of all study plots by willets between early and late winter (Table 2: Seasons) resulted primarily from mid-season influxes onto aquaculture plots (Table 1; $F = 29.92$, $df = 1, 118$, $P < 0.001$). Smaller early-to-late winter increases of willets occurred on control plots (Table 1; $F = 9.46$, $df = 1, 238$, $P = 0.002$). We found no general baywide intraseasonal increase (pooled across years) in willet numbers on Tomales Bay ($F = 1.75$, $df = 1, 27$, $P = 0.20$), and no significant baywide intraseasonal differences were found within individual years (all years: $P > 0.05$; Kelly[2] 1990-94).

A significant early-to-late winter difference in the use of study plots by marbled godwits (Table 2) also resulted from mid-season increases on aquaculture plots (Table 1; $F = 8.23$, $df = 1,118$, $P = 0.005$); early-to-late winter differences on control plots were not significant (Table 1; $F = 0.58$, $df = 1, 238$, $P = 0.45$). We found no general baywide intraseasonal increase (pooled across years) in the numbers of marbled godwits ($F = 0.56$, $df = 1,27$, $P = 0.46$); within years, marbled godwits increased only in 1990-91 ($F = 35.04$, $P < 0.01$, $df = 1,3$; Kelly[2] 1990-94).

Interactions between areas, seasons, and years accounted for some of the variability of shorebird abundance. Differences in abundance of black-bellied plovers, willets, and least sandpipers between control and aquaculture areas were partly dependent on winter timing (Table 2: Areas x Seasons). Differences in abundance of black-bellied plovers and marbled godwits between control and aquaculture

areas were partly dependent on differences among years (Table 2: Areas x Years). Winter timing influenced the abundance of black-bellied plovers on control and aquaculture areas differently among years (Table 2: Areas x Seasons x Years).

Comparisons of shorebird abundance among control plots showed no underlying habitat gradients, and additional analyses using subsets of controls were consistent with our initial results. Habitat use did not differ between the inner (Plots 1 and 6) and outer (Plots 2 and 5) portions of the control area for all species analyzed (P ranging from 0.45 to 0.88), except for sanderling, which was significantly more abundant on outer control plots than on inner control plots (likelihood ratio = 4.11, P = 0.043). Habitat use by black-bellied plover, willet, marbled godwit, sanderling, and dunlin did not differ between the northwest and southeast sides of the delta (P ranging from 0.06 to 0.88). Western sandpipers and least sandpipers used the northwest side of the delta significantly more than the southeast side (likelihood ratios = 6.78 and 8.53; P < 0.01). An additional ANCOVA using only control plots on the southeast side of the delta, where western sandpiper abundance was lower, was consistent with the initial results based on all four control plots, showing significant avoidance of the aquaculture area (likelihood ratio = 8.04, P < 0.01). ANCOVA using only control plots on the northwest side, and in a separate analysis, only control plots on the southeast side of the delta confirmed the absence of significant aquaculture effects on least sandpiper abundance (P > 0.05). Although dunlin abundance did not differ significantly between control areas on the two sides of the delta (P = 0.06), mean values were higher on the southeast side. ANCOVA based only on control plots on the northwest side of the delta confirmed our initial results showing significant avoidance of the aquaculture area by dunlins (likelihood ratio = 4.02, P = 0.045).

The presence of aquaculture equipment on up to 15% of Plot 6 in 1992-93 did not influence the overall results. Shorebird abundance on Plot 6 did not differ (P > 0.05) between 1992-93 and the other 4 years of study, and except for willets, did not differ (P > 0.05) from other control plots in 1992-93. Willets were significantly more abundant on Plot 6 in 1992-93 than on the other control plots (likelihood ratio = 4.19, P = 0.041) as a result of the regular occurrence of one individual in the vicinity of the oyster racks (J. Kelly, pers. obs.). ANCOVA models generated for each species after removing the 1992-93 Plot 6 data produced the same significant effects as the original analyses. However, the strength of significant

aquaculture effects increased; probabilities that the observed aquaculture effects on abundance of western sandpipers, dunlins, and willets were random were further reduced (likelihood ratios = 5.62, 8.13, 15.10; P = 0.022, 0.004, 0.0001; cf Table 2).

Species richness did not differ between control and aquaculture plots (likelihood ratio = 0.007, P = 0.93). We also found no significant difference in proportional species diversity, based on the Shannon index, between control and aquaculture plots (likelihood ratio = 0.616, P = 0.43).

DISCUSSION

Wintering western sandpipers and dunlins avoided aquaculture areas, whereas willets favored these areas. These differences were not the result of underlying spatial variation detectable among plots nested within areas. However, we must consider the alternative hypothesis that observed differences between control and aquaculture areas resulted from underlying (pre-aquaculture) habitat conditions along a larger habitat gradient. Although our study did not have a complete set of temporal treatments to control for larger spatial effects, aquaculture development on up to 15% of Plot 6 in 1992-93 influenced the strength of the results. Shorebird use of Plot 6 in 1992-93 was not significantly different from other control plots or years, but the higher significance levels that resulted from the removal of 1992-93 Plot 6 data were consistent with our other results, suggesting that aquaculture effects were independent of underlying spatial gradients. We emphasize, however, the need for further corroboration using more complete temporal controls.

Differences in shorebird densities have been related to differences in foraging substrate types (Page et al. 1979, Myers et al 1980, Quammen 1982, 1984, Hinklin and Smith 1984, Yates et al. 1993). Existing evidence suggests that pre-aquaculture substrates were similar among plots. Before the development of the aquaculture area, surface sediments at Walker Creek Delta were composed of fine sands, silts, and clays; "clayey silts" (> 50% silt; median grain size = 0.004 - 0.063 mm) dominated the entire study area, with transitional occurrences of poorly sorted "sand-silt-clay" (< 50% of each class; median grain size = 0.063 - 0.250 mm) on the southwest edge of the delta, primarily below MLLW

(Daetwyler 1966). Therefore, pre-aquaculture substrates could have had an increasing proportion of fine sands on the outer edge of the delta, but primarily below the lower edge (MLLW) of the study plots. Further evidence that possible pre-aquaculture sediment gradients did not affect our results was found in the absence of underlying habitat use gradients between control plots on the inner and outer delta. Substrates did not appear to differ among study plots, although we did not measure sediment characteristics during the present study. Some accumulations of very fine unconsolidated material characteristic of oyster pseudofeces (Day et al. 1987, p. 368) were occasionally observed in the aquaculture plots (J. Kelly, pers. obs.).

Shorebird density and distribution often varies with the density of prey (Goss-Custard 1977, Connors et al. 1981, Hinklin and Smith 1984, Evans and Dugan 1984, Wilson 1990, Colwell and Landrum 1993). However, pre-aquaculture substrate conditions in the vicinity of our study (Daetwyler 1966) may not have been associated with measurable differences in prey species composition, diversity, or density. Johnson (1971) reported that it is rarely possible in Tomales Bay to demonstrate a high correlation between the abundance or distribution of invertebrate species and a specific property of the sediment such as particle size. Juskevice[4] (1969) found positive correlations in Tomales Bay between the abundance of a few invertebrate species and particle size, but only within a narrow range of particle sizes. Therefore, existing evidence suggests that significant pre-aquaculture habitat differences between control and treatment plots may not have been detectable. Nevertheless, without more extensive temporal treatment of control areas, our results only suggest that aquaculture effects on shorebirds were independent of underlying spatial habitat differences.

Hypotheses that could explain factors or processes responsible for the observed differences in shorebird abundance between aquaculture and control areas were not tested in this study. Such hypotheses include reduced or increased foraging opportunities related to (i) aquaculture-induced changes in the abundance or availability of preferred prey (Triani[1] 1994), (ii) alteration of foraging substrates related to aquaculture-induced accumulation of pseudofeces or other sediments (Day et al. 1987: 368; Deslous-Paoli et al. 1992), (iii) alteration of foraging substrates associated with foot traffic by oyster growers, maintenance of stakes and bags, or other aquaculture related activities, (iv) selection or

avoidance of oyster bags or racks as foraging substrates, (v) differences in opportunities for group foraging or territoriality resulting from the interruption of open foraging areas by oyster bags and racks, or (vi) differences in risk of predation by raptors.

On numerous occasions, we observed least sandpipers foraging on top of oyster bags as well as on sediments below elevated oyster bags; in contrast, western sandpipers and dunlins generally foraged under or between rows of oyster bags. The primary foraging method used by least sandpipers is pecking at the substrate surface (Baker and Baker 1973), which probably involves visual cues. An emphasis on visual searching and surface feeding may allow least sandpipers to exploit the surfaces of oyster bags and racks and may account for the absence of significant differences in their abundance between control and aquaculture areas. In contrast, dunlins (Baker and Baker 1973) and western sandpipers (Recher 1966, Ashmole 1970) forage more often by probing into substrates and may therefore be less suited for feeding on or around oyster bags and racks. These behavioral differences could account for the reduced abundance of western sandpipers and dunlins we observed in the aquaculture area.

Our results suggest that willets preferred areas with aquaculture activity as feeding areas in winter. We often saw willets foraging on or between aquaculture structures, suggesting enhanced foraging opportunities for willets in these areas. Willets are known to use a wide variety of foraging habitats and prey species, and may show seasonal changes in diet (Recher 1966, Stenzel et al. 1976, Page et al. 1979, Kelly and Cogswell 1979). Our results also suggest that willets may exploit aquaculture areas to a greater extent as winter progresses, perhaps opportunistically as food availability or competition for food changes among habitat areas.

Western sandpipers or dunlins may be at greater risk of predation by raptors in aquaculture areas than on open tidal flats because of (i) reduced visibility and delayed detection of approaching predators in aquaculture areas, (ii) increased predation pressure related to the use of aquaculture equipment for perches by predators, or (iii) disruption of antipredator flocking behavior (Page and Whitacre 1975, Kus et al. 1984) related to the interruption of open foraging areas by oyster bags and racks. In spite of these possibilities, foraging least sandpipers remained on the ground beneath elevated oyster racks during attacks by a peregrine falcon, *Falco peregrinus* (J. Kelly, pers. obs.), suggesting that aquaculture areas

provide increased cover that may protect some species from predation.

Several authors have provided evidence that shorebird populations may be limited by foraging opportunities or habitat modification during winter (Baker and Baker 1973, Goss-Custard 1979, 1984, Evans and Pienkowski 1984, Senner and Howe 1984, Goss-Custard et al. 1995). Evans (1991) estimated that most mortality in dunlins (76%) occurs during the nonbreeding season. In our study, avoidance of aquaculture plots by western sandpipers and dunlins substantially outweighed the selection of aquaculture areas by willets (Table 1). If shorebirds are limited by wintering habitat, changes in habitat use may reflect population effects. When we scaled observed differences in shorebird use to population sizes on Tomales Bay (mean baywide winter abundances of 400, 6033, and 1851 for willet, dunlin, and western sandpiper, respectively; Kelly[2] 1990-94), average decreases in dunlin and western sandpiper on aquaculture plots were 1.52 and 1.18 times greater, respectively, than the relative <u>increase</u> observed in willets. When scaled to estimated Pacific Flyway populations (70,000, 450,000-600,000, and 1,300,000 for willet, dunlin, and western sandpiper, respectively; Page and Gill 1994), the average decrease in dunlin was 2.70-3.51 times greater than the increase in willet, whereas the proportional decrease in western sandpiper, the most abundant shorebird species in the Pacific Flyway, was only 0.30 times the increase in willet. We emphasize that these comparisons are based on rough population estimates and should be interpreted cautiously.

Existing evidence suggests that (i) foraging shorebirds generally concentrate along the edge of the falling or rising tide (Recher 1966, Evans and Dugan 1984), (ii) oyster growers concentrate their operations on intertidal strata with particular tidal exposure regimes, generally below 0.3 m MLLW (pers. obs.), (iii) small losses in the extent or quality of available feeding habitat could result in proportionally greater decreases in wintering shorebird populations (Myers et al. 1979, Goss-Custard 1979, Senner and Howe 1984), and (iv) the two most abundant shorebird species on Tomales Bay (Kelly[2] 1990-94) and other coastal wetlands of the Pacific Flyway (Kjelmyr et al.[5] 1991) significantly avoided areas used for aquaculture on Tomales Bay (this study). Therefore, foraging opportunities for some species may be particularly limited when tide levels coincide with elevational strata preferred for growing oysters. Although willets may forage preferentially in these areas, and species diversity based on proportional abundances is

not significantly affected, our results suggest a net decrease in overall shorebird use of open tidal flats developed for aquaculture.

ACKNOWLEDGMENTS

This study was made possible by the expert field assistance of R. Macdonald, T. Nordbye, D. Reinking, F. Tomlinson, and C. Wood. Valuable help in developing the sampling design was provided by F. Botti, P. Connors, J. Finger, P. Kelly, J. Maron, and G. Page. We thank D. Oman for helpful comments on the statistical analysis and P. Connors, D Kohlhorst, J. Orsi, and an anonymous reviewer for several suggestions that improved the manuscript. S. Tappen assisted in the preparation of figures and tables. This study was funded by Contracts FG9519, FG1163, and FG3113WM with the California Department of Fish and Game.

LITERATURE CITED

Ashmole, M. J. 1970. Feeding of western and semipalmated sandpipers in Peruvian winter quarters. Auk 87:131-135.

Baker, M. C. and A. E. M. Baker. 1973. Niche relationships among six species of shorebirds on their wintering and breeding ranges. Ecological Monographs 43:193-212.

Bryant, D. M. 1979. Effects of prey density and site character on estuary usage by overwintering waders (Charadrii). Estuarine and Coastal Marine Science 9:369-384.

Burger, J. 1984a. Shorebirds as marine animals. Pages 17-81 *in:* J. Burger and B. L. Olla, editors. Behavior of marine animals. Volume 5. Breeding behavior and populations. Plenum Press, New York, New York, USA.

Burger, J. 1984b. Abiotic factors affecting migrant shorebirds. Pages 1-72 *in:* J. Burger and B. L. Olla, editors. Behavior of marine animals. Vol. 6. Migration and foraging behavior. Plenum Press, New York, New York, USA.

Colwell, M. A. and S. L. Landrum. 1993. Nonrandom shorebird distribution and fine-scale variation in prey abundance. Condor 95:94-103.

Connors, P. G., J. P. Myers, C. S. W. Connors, and F. A. Pitelka. 1981. Interhabitat movements by sanderlings in relation to foraging profitability and the tidal cycle. Auk 98:49-64.

Daetwyler, C. C. 1966. Marine geology of Tomales Bay. Scripps Institution of Oceanography and Pacific Marine Station, University of the Pacific, Research Report No. 6.

Day, J. W., Jr., C. A. S. Hall, W. M. Kemp, and A. Yanez-Arancibia. 1987. Estuarine ecology. John Wiley and Sons, New York, New York, USA.

Deslous-Paoli, J. M., A. M. Lannou, and P. Geairon. 1992. Effects of the feeding behaviour of *Crassostrea gigas* (Bivalve Molluscs) on biosedimentation of natural particulate matter. Hydrobiologia 231:85.

Dixon, W. J. (editor). 1992. BMDP statistical software manual, Volume 2. University of California Press, Berkeley, California, USA.

Evans, P. R. 1991. Seasonal and annual patterns of mortality in migratory shorebirds: some conservation implications. Pages 346-359 *in:* C. H. Perrins, J. D, Goss-Custard, and G. J. M Herons, editors. Bird population studies. Oxford University Press, Oxford, England.

Evans, P. R. and P. J. Dugan. 1984. Coastal birds: numbers in relation to food resources. Pages 8-28 *in:* P. R. Evans, J. D. Goss-Custard, and W. G. Hale, editors. Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge, Massachusetts, USA.

Evans, P. R and M. W. Pienkowski. 1984. Population dynamics of shorebirds. Pages 83-123 *in:* J. Burger and B. L. Olla, editors. Behavior of marine animals. Volume 5. Breeding behavior and populations. Plenum Press, New York, New York, USA.

Gerstenberg, R. H. 1979. Habitat utilization by wintering and migrating shorebirds on Humboldt Bay, California. Studies in Avian Biol. No. 2:33-40.

Goss-Custard, J. D. 1970. The responses of redshank (*Tringa totanus* (L.)) to spatial variations in the density of their prey. Journal of Animal Ecology 39:91-113.

Goss-Custard, J. D. 1977. The density of migratory and overwintering redshank, *Tringa totanus* (L.) and

curlew, *Numenius arquata* (L.) in relation to density of their prey in South-east England. Estuarine and Coastal Marine Science 5:497-510.

Goss-Custard, J. D. 1979. Effect of habitat loss on the numbers of overwintering shorebirds. Studies in Avian Biology 2:167-177.

Goss-Custard, J. D. 1984. Intake rates and food supply in migrating and wintering shorebirds. Pages 233-270 *in*: J. Burger and B. L. Olla, editors. Behavior of marine animals. Vol. 6: Shorebirds, migration and foraging behavior. Plenum Press, New York, New York, USA.

Goss-Custard, J. D., R. W. G. Caldow, R. T. Clarke, and A. D. West. 1995. Deriving population parameters from individual variations in foraging behavior. II. Model tests and population parameters. Journal of Animal Ecology 64:277-289.

Hinklin, P. W. and P. C. Smith. 1984. Selection of foraging sites and invertebrate prey by migrant semipalmated sandpipers, *Calidris pusilla* (Pallas), in Minas Basin, Bay of Fundy. Canadian Journal of Zoology 62:2201-2210.

Johnson, R. G. 1971. Animal-sediment relations in shallow water benthic communities. Marine Geology 11:93-104.

Kelly, P. R. and H. L. Cogswell. 1979. Movements and habitat use by wintering populations of willets and marbled godwits. Studies in Avian Biology 2:69-82.

Kus, B. E., P. Ashman, G. W. Page, and L. E. Stenzel. 1984. Age-related mortality in a wintering population of dunlin. Auk 101:69-73.

Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey, USA.

Meire, P., and E. Kuyken. 1984. Relations between distributions of waders and the intertidal benthic fauna of the Oosterschelde, Netherlands. Pages 57-68 *in*: P. R. Evans, J. D. Goss-Custard, and W. G. Hale, editors. 1984. Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge, Massachusetts, USA.

Myers, J. P. 1984. Spacing behavior of nonbreeding shorebirds. Pages 271-321 *in*: J. Burger and B. L. Olla, editors. Behavior of marine animals. Vol. 6: Shorebirds, migration and foraging behavior.

Plenum Press, New York, New York, USA.

Myers, J. P., P. G. Connors, and F. A. Pitelka. 1979. Territory size in wintering sanderlings: the effects of prey abundance and intruder density. Auk 96:551-561.

Myers, J. P., S. L. Williams, and F. A. Pitelka. 1980. An experimental analysis of prey availability for sanderlings (Aves: Scolopacidae) feeding on sandy beach crustaceans. Canadian Journal of Zoology 58:1565-1574.

Ottmann, F. and J. M. Sornin. 1985. Observations on sediment accumulation as a result of mollusk culture systems in France. Pages 329-337 *in:* N. Labish Chao and W. Kirby-Smith, editors. 1985. Proceedings of the international symposium on utilization of coastal ecosystems: planning, pollution and productivity, Volume 1. Taken from: Hanfman, D. E. Coleman, and S. J. Tibbitt. 1991. Interactions of aquaculture, marine coastal ecosystems, and near-shore waters: a bibliography. National Agricultural Library, Beltsville, Maryland, USA (abstract no. 118).

Page, G. W. and R. E. Gill. 1994. Shorebirds in western North America: late 1800s to late 1900s. Studies in Avian Biology 15:147-160.

Page, G., L. E. Stenzel, and C. M. Wolfe. 1979. Aspects of the occurrence of shorebirds on a central California estuary. Studies in Avian Biology 2:15-32.

Page, G. and D. F. Whitacre. 1975. Raptor predation on wintering shorebirds. Condor 77:73-83.

Puttick, G. M. 1984. Foraging and activity patterns of wintering shorebirds. Pages 203-232 *in*: J. Burger and B. L. Olla, editors. Behavior of marine animals. Vol. 6: Shorebirds, migration and foraging behavior. Plenum Press, New York, New York, USA.

Quammen, M. L. 1982. Influence of subtle substrate differences on feeding by shorebirds on intertidal mudflats. Marine Biology 71:339-343.

Quammen, M. L. 1984. Predation by shorebirds, fish, and crabs on invertebrates in intertidal mudflats: an experimental test. Ecology 65:529-537.

Recher, H. F. 1966. Some Aspects of the Ecology of Migrant Shorebirds. Ecology 47:393-407.

Senner, S. E. and M. A. Howe. 1984. Conservation of nearctic shorebirds. Pages 379-421 *in:* J. Burger and B. L. Olla, editors. Behavior of marine animals. Volume 5. Breeding behavior and

populations. Plenum Press, New York, New York, USA.

Stenzel, L. E., H. R. Huber, and G. W. Page. 1976. Feeding Behavior of the Long-billed Curlew and willet. Wilson Bulletin 88:314-332.

Wilson, W. H. 1990. Relationships between prey abundance and foraging site selection by semipalmated sandpipers on a Bay of Fundy mudflat. Journal of Field Ornithology. 61:9-19.

Yates, M. G., J. D. Goss-Custard, S. McGrorty, K. H. Ladhani, S. E. A. Le V. Dit Durell, R. t. Clarke, W. E. Rispin, I. Moy, t. Yates, R. A. Plant, and A. J. Frost. 1993. Sediment characteristics, invertebrate densities and shorebird densities on the inner banks of the Wash. Journal of Applied Ecology 30:599-614.

FOOTNOTES

[1]Triani, M. 1994. Influence of oyster culture methods on benthic infauna of Humboldt Bay, California. Draft M.S. Thesis, Humboldt State University, Arcata, California, USA.

[2]Kelly, J. P. 1990-94. Annual report of the Tomales Bay shorebird census. ACR Project Reports 89-4-1, 89-4-2,89-4-3,89-4-4, and 89-4-5, Audubon Canyon Ranch, Stinson Beach, California, USA..

[3]Kelly, J. P. 1990. 1989-90 winter and spring shorebird abundances on Tomales Bay, California, and notes on the movements of shorebirds within Tomales Bay. ACR Project Report 89-4-1, Audubon Canyon Ranch, Stinson Beach, California, USA.

[4]Juskevice, J. A. 1969. Interspecific correlation and association in benthic marine communities. Ph.D. Dissertation, University of Chicago, Illinois, USA.

[5]Kjelmyr, J., G. W. Page, W. D. Shuford, and L. E. Stenzel. 1991. Shorebird numbers in wetlands of the Pacific Flyway: a summary of spring, fall, and winter counts in 1988, 1989, and 1990. Report of the Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, California, USA.

Table 1. Means and 95% confidence intervals of means (L_1 - L_2) of shorebird abundances on study plots from 1989-90 to 1993-94 at Walker Creek Delta, Tomales Bay, California; n = 116 and 124 on early winter (EW) and late winter (LW) control plots, and 58 and 62 on EW and LW aquaculture plots. Confidence intervals are asymmetric because values are transformed back into linear scale from log-transformed data.

		Control			Aquaculture		
Species		Mean	L_1 -	L_2	Mean	L_1 -	L_2
Black-bellied Plover	EW	0.91	0.65 -	1.22	1.36	0.81 -	2.08
	LW	0.99	0.71 -	1.32	0.43	0.23 -	0.68
Greater Yellowlegs	EW	0.00	0.00 -	0.00	0.02	-0.01 -	0.06
	LW	0.00	0.00 -	0.00	0.00	0.00 -	0.00
Willet	EW	0.42	0.28 -	0.58	1.45	0.87 -	2.20
	LW	0.84	0.63 -	1.08	5.03	4.01 -	6.27
Marbled Godwit	EW	2.44	1.53 -	3.66	1.27	0.57 -	2.28
	LW	3.01	2.10 -	4.19	4.15	2.39 -	6.81
Ruddy Turnstone	EW	0.02	0.00 -	0.03	0.12	0.05 -	0.20
	LW	0.01	0.00 -	0.02	0.02	0.00 -	0.04
Black Turnstone	EW	0.08	0.03 -	0.13	0.31	0.13 -	0.53
	LW	0.00	0.00 -	0.00	0.02	-0.01 -	0.05

Table 1. continued

Species		Control Mean	Control L_1 - L_2	Aquaculture Mean	Aquaculture L_1 - L_2
Sanderling	EW	1.82	1.14 - 2.72	2.48	1.27 - 4.34
	LW	0.81	0.51 - 1.17	2.09	1.14 - 3.45
Western Sandpiper	EW	23.63	16.28 - 34.10	2.99	1.60 - 5.15
	LW	9.83	6.14 - 15.41	1.80	0.90 - 3.13
Least Sandpiper	EW	36.61	24.98 - 53.44	9.20	4.95 - 16.48
	LW	9.61	6.01 - 15.07	10.86	6.25 - 18.39
Dunlin	EW	111.72	69.88 - 178.26	9.12	4.63 - 17.20
	LW	23.24	13.91 - 38.40	5.97	3.09 - 10.88
Long-billed Dowitcher	EW	0.00	0.00 - 0.00	0.00	0.00 - 0.00
	LW	0.05	-0.02 - 0.12	0.00	0.00 - 0.00
Short-billed Dowitcher	EW	0.11	0.03 - 0.20	0.09	0.01 - 0.17
	LW	0.002	0.00 - 0.01	0.01	0.01 - 0.02
Dowitcher (undifferentiated)	EW	0.12	0.05 - 0.20	0.37	0.13 - 0.65
	LW	0.02	-0.01 - 0.05	0.12	0.02 - 0.23
Gull species (covariate)	EW	64.22	43.49 - 94.62	160.99	112.23 - 230.75
	LW	154.27	113.37 - 209.80	74.91	49.89 -112.24

Table 2. Components of variation of log-transformed winter shorebird abundance at Walker Creek Delta, Tomales Bay, California. Analysis of Covariance was used to control for the displacement of shorebirds by gulls.

Source of variation	Black-bellied Plover	Willet	Marbled Godwit	Sanderling	Western Sandpiper	Least Sandpiper	Dunlin
AREAS (control vs. aquaculture)							
Parameter Estimate	0.014	-0.189	0.016	-0.080	0.344	0.126	0.395
Standard Error	0.032	0.036	0.060	0.121	0.154	0.181	0.125
Likelihood Ratio χ^2 (df=1)	0.183	10.952***	0.069	0.427	3.914*	0.479	6.159*
PLOTS (nested within AREAS)							
Parameter Estimate	0.002	0.004	0.009	0.038	0.076	0.099	0.025
Standard Error	0.002	0.003	0.009	0.028	0.056	0.071	0.025
Likelihood Ratio χ^2 (df=1)	2.654	7.661**	4.586*	35.753***	27.331***	32.703***	4.108*
YEARS							
Parameter Estimate	0.041	0.002	0.143	0.065	0.035	0.000	0.285
Standard Error	0.028	0.009	0.102	0.074	0.073	0.000	0.240
Likelihood Ratio χ^2 (df=1)	11.073***	0.081	6.442*	1.169	0.288	0.000	3.286

Table 2. continued

Source of variation	Black-bellied Plover	Willet	Marbled Godwit	Sanderling	Western Sandpiper	Least Sandpiper	Dunlin
SEASONS (early vs. late winter)							
Parameter Estimate	0.041	-0.132	-0.124	0.052	0.118	0.114	0.185
Standard Error	0.024	0.038	0.050	0.035	0.070	0.050	0.090
Likelihood Ratio χ^2 (df=1)	2.575	7.030**	4.082*	1.826	2.281	3.745	3.119
AREAS X SEASONS							
Parameter Estimate	-0.062	0.062	0.059	0.044	0.035	0.125	0.103
Standard Error	-0.024	0.022	0.036	0.027	0.054	0.046	0.048
Likelihood Ratio χ^2 (df=1)	5.319*	5.465*	2.141	2.706	0.404	6.045*	3.520
AREAS X YEARS							
Parameter Estimate	0.000	0.001	0.006	0.068	0.066	0.121	0.088
Standard Error	0.000	0.005	0.015	0.051	0.067	0.070	0.073
Likelihood Ratio χ^2 (df=1)	0.000	0.063	0.177	9.307**	1.819	7.168**	3.192

Table 2. continued

Source of variation	Black-bellied Plover	Willet	Marbled Godwit	Sanderling	Western Sandpiper	Least Sandpiper	Dunlin
SEASONS X YEARS							
Parameter Estimate	0.000	0.010	0.012	0.006	0.020	0.005	0.059
Standard Error	0.000	0.010	0.017	0.007	0.035	0.014	0.049
Likelihood Ratio χ^2 (df=1)	0.000	2.185	0.648	1.210	0.318	0.195	2.083
AREAS X SEASONS X YEARS							
Parameter Estimate	0.006	0.004	0.008	0.000	0.023	0.000	0.000
Standard Error	0.004	0.006	0.016	0.000	0.035	0.000	0.000
Likelihood Ratio χ^2 (df=1)	4.496*	1.108	0.495	0.000	0.883	0.000	0.000
GULLS: Covariate							
Parameter Estimate	-0.018	-0.057	-0.073	0.016	-0.087	-0.156	-0.112
Standard Error	0.023	0.023	0.041	0.038	0.060	0.065	0.066
Likelihood Ratio χ^2 (df=1)	0.599	5.796*	2.996	0.164	1.998	5.599*	2.601

* P < 0.05, ** P < 0.01, *** P < 0.001

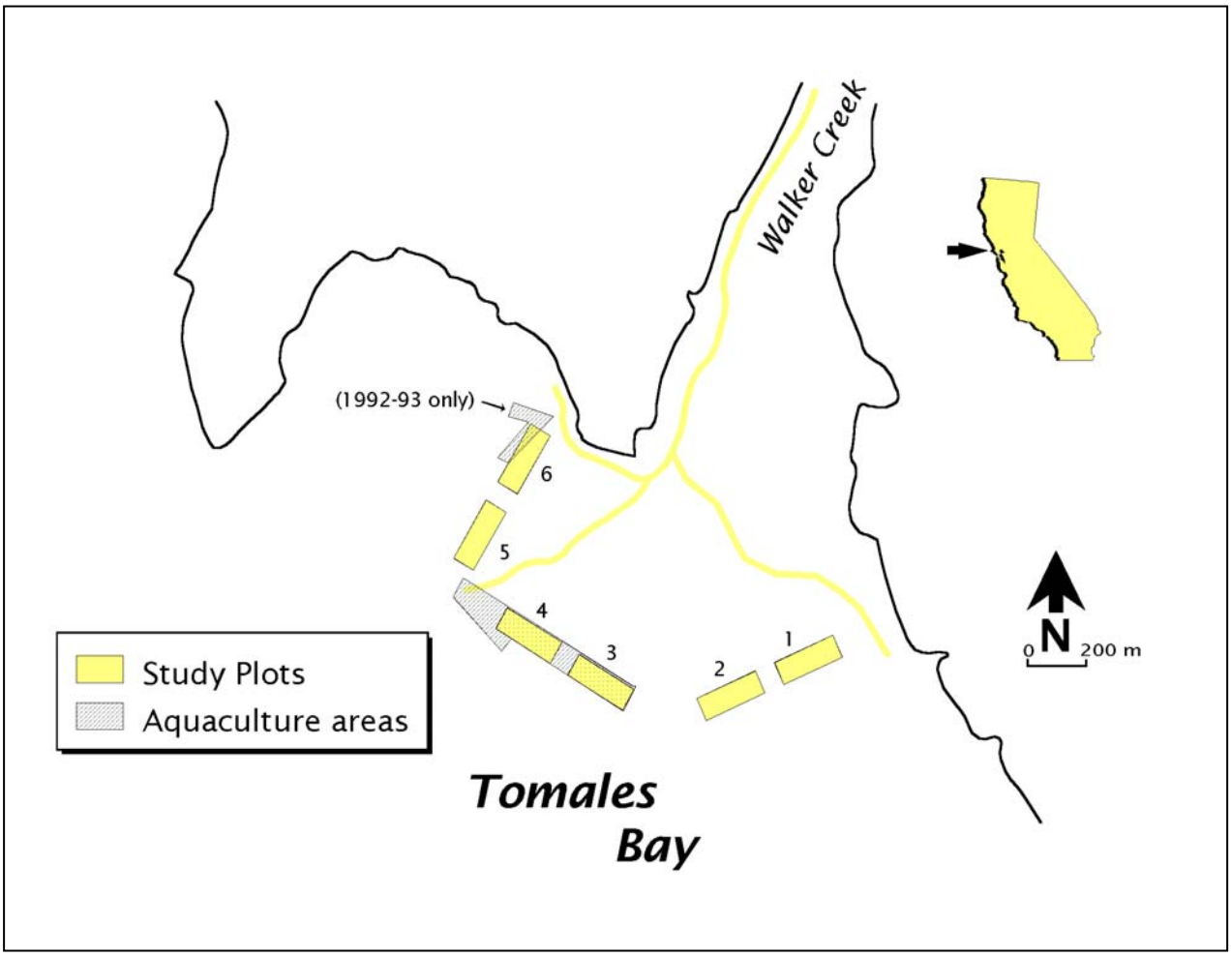

Figure 1. Shorebird study plots and aquaculture lease areas at Walker Creek Delta, Tomales Bay, California. Gray lines show the stream channels.