NONRANDOM SHOREBIRD DISTRIBUTION AND FINE-SCALE VARIATION IN PREY ABUNDANCE[1]

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Abstract. Spatial variation in the abundance of nonbreeding shorebirds can be predicted to varying degrees by the density of their prey species; strongest relationships obtain from studies encompassing large spatial scales (e.g., entire estuaries). We examined variation in shorebird distribution and abundance within microhabitats of the Mad River estuary, California, with the following null hypotheses: (1) shorebird spatial distribution was random, and (2) no relationship existed between bird abundance and invertebrate densities. Shorebirds exhibited nonrandom spatial distributions; species were highly clumped within the study area. Most foraging calidridine sandpipers (*Calidris minutilla, C. mauri,* and *C. bairdii*) aggregated in sandy areas within 1 m of the tide edge, where they foraged by probing for a burrow-dwelling amphipod, *Corophium* spp. By contrast, Semipalmated Plovers (*Charadrius semipalmatus*) and especially Ruddy Turnstones (*Arenaria interpres*) foraged by pecking in drier, coarse-grained substrates greater than 1 m from the tide edge. *Corophium* densities in sand exceeded those in cobble; *Corophium* densities explained significant variation (r^2 = 0.36, 0.31 and 0.22) in the abundance of Least Sandpipers, Western Sandpipers and all shorebirds, respectively. These findings emphasize the importance of understanding variation in processes across spatial scales.

Key words: shorebirds; numerical relationship; estuaries; invertebrates; nonbreeding distributions.

INTRODUCTION

The influence of food resources on the ecology of nonbreeding shorebirds in coastal environments has been well-studied (see Burger and Olla 1984, Evans et al. 1984). Shorebirds interact with prey in two ways, equivalent to functional and numerical responses of predators (Goss-Custard 1977). In the first case, variation in prey abundance may influence foraging behavior and social interactions of birds, which affects the rate at which prey are consumed. Additionally, prey abundance may influence spacing of individuals (see reviews by Goss-Custard 1984, Puttick 1984). Second, and pertinent to this study, variation in prey abundance may affect the distribution of nonbreeding shorebirds within estuaries and among habitats (see Evans and Dugan 1984).

Shorebird distributions are strongly influenced by food (Evans and Dugan 1984), especially during the nonbreeding season when invertebrate prey abundance often decreases and energetic costs associated with maintenance and migration increase (Evans 1976, Kersten and Piersma 1987). Numerous studies have demonstrated a positive correlation between shorebird abundance and invertebrate prey densities, especially when patterns are examined across large spatial scales (e.g., encompassing entire estuaries; Goss-Custard 1970, Bryant 1979, Hicklin and Smith 1984, Meire and Kuyken 1984). However, the few analyses of the relationship between shorebird abundance and prey densities conducted on finer spatial scales (e.g., across sampling stations spaced 10–100 m apart) obtained either weak (Bengston and Svensson 1968, Wilson 1990) or inverse (Kelsey and Hassall 1989) numerical relationships.

In this paper, we examine fine-scale variation in the spatial distribution and foraging ecology of a group of nonbreeding shorebirds with the following objectives. First, we examine the ecology of foraging shorebirds in association with a null model of random spatial distribution of birds. Second, we evaluate the numerical relationship between shorebird abundances and invertebrate densities. Finally, we compare our findings with those from other studies of nonbreeding shorebirds and we discuss the influence of spatial scale on shorebird-prey relationships.

STUDY AREA AND METHODS

We studied shorebirds along an intertidal stretch of the Mad River, approximately 4 km upstream from the confluence of the river and Pacific Ocean
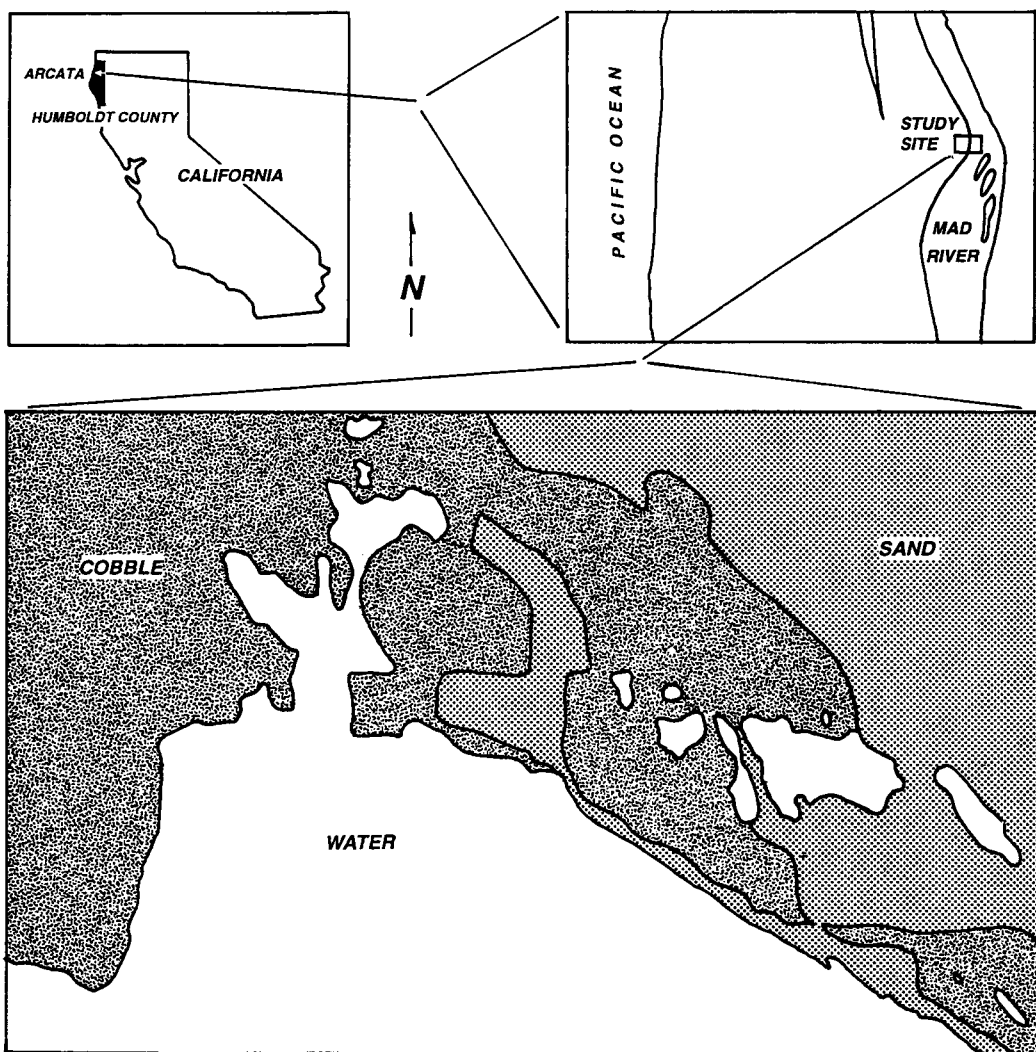
FIGURE 1.   Location of study area within the Mad River estuary, Humboldt County, California.

in Humboldt County, California (Fig. 1). Within the study area, the Mad River flows north parallel to the ocean and adjacent to cliffs. To the west of the river lie gently sloping intertidal flats, consisting mostly of unvegetated substrates varying in particle size from silt to cobble. Sandy substrates predominate downstream from a riffle that flows through cobble substrates at low tide. Prior to observations of birds and invertebrate sampling, we established a 25 × 40 m study grid (Fig. 1), subdivided into 25 m² sections by steel rods placed at 5 m intervals. Twelve of 40 grid sections lay under water at low tide; we confined our study to sections ($n = 28$) not inundated at low tide. For each grid section, we mapped features of the substrate, topography and invertebrate concentrations.

We observed shorebirds between 27 July and 24 September 1991 ($n = 24$ observation periods) from atop a 2 m river bank situated about 35 m east of the study grid using 7 × 50 mm binoculars and a 22× spotting scope. Our study ended when a storm altered a sand bar at the mouth of the river, which raised low-water conditions within the estuary and altered features of the study area. We conducted observations between 07:00 and 13:00 during slack low tide using a scan sampling technique (Altmann 1974); observations ended

when the tidal edge first advanced. We scanned birds at 15-min intervals, beginning at one end of the site and panning to the opposite end until we had tallied all birds within the study grid. For each bird, we recorded the following: (1) species; (2) location on study grid to nearest 1 m; (3) substrate (cobble or sand); (4) proximity to the tide edge (> or <1 m from tide edge); (5) wading depth (0 cm, 0–2 cm, >2 cm); and (6) foraging behavior. We categorized birds as using one of the following foraging techniques: (1) *single peck,* taking surface prey with one jab of the bill; (2) *flip peck,* turning over rocks and jabbing once with the bill; (3) *multiple pecks,* repeatedly and rapidly pecking prey from the surface; (4) *single probe,* inserting the bill into the substrate once to extract prey; and (5) *multiple probe,* probing with a rapid, repetitive action.

We determined invertebrate densities by extracting 1–5 core samples (10.5 cm diameter cylinder pushed 10 cm into the substrate) from random locations within each 25 m² grid section throughout the period in which birds were observed. We sorted invertebrates using a 0.423 mm soil sieve and preserved them in formalin. Following extraction of invertebrates, we dried and weighed the substrate from each core sample. We characterized each sample by passing it through a series of five U.S. standard soil testing sieves (mesh sizes: 25 mm; 12.5 mm; 2.0 mm; 1.0 mm; and 0.5 mm), shaking each sample 300 times. We weighed the substrated remaining in each of the three largest sieves and processed the remainder of the sample by shaking it an additional 100 times in each of the smaller sieves. We recorded the percentage by weight of each substrate size within a sample. From these data we derived an index of substrate composition by multiplying percentages of the substrate types by their rank (1–5) in order of smallest to largest components. The sum of these products yielded an index value with a possible range of 1.00–5.00.

We examined patterns (random, clumped, even) of spatial distribution of the five most abundant shorebird species by summing bird observations in each 25 m² grid section and calculating the $\bar{x}$ density and s^2 for all 28 grid sections. We compared observed ratios of s^2:$\bar{x}$ to a random distribution (where s^2:$\bar{x} = 1$) using t-tests. We analyzed the relationship between bird abundance and invertebrate densities at two levels. First, within each 25 m² section of the grid ($n =$

28), we summed observations of Least and Western sandpipers (the only species with sufficient observations to warrant analysis) and compared them with the average densities of invertebrates from cores sampled within the grid section. On a finer spatial scale, we totaled all shorebird observations within 1 m of each core sample and compared these data with invertebrate densities. For both analyses, we used stepwise multiple regression to analyze the numerical relationship between birds (dependent variable) and invertebrates (independent variables) (SAS 1985). When necessary, we logarithmically transformed data to meet assumptions of normality and homogeneity of variances. In some cases (e.g., densities of marine worms and unidentified invertebrates) transformations could not correct such problems in the data and we carried out analyses on the original, untransformed data. We analyzed categorical data using G-tests (SAS 1985).

RESULTS

Bird observations. We observed 11 species and 689 birds (8 shorebird species and 682 shorebirds) on the study grid during 24 observation periods (Table 1). Least Sandpipers (*Calidris minutilla*) and Western Sandpipers (*C. mauri*) comprised 89% of observations; and combined with Semipalmated Plovers (*Charadrius semipalmatus*), Ruddy Turnstones (*Arenaria interpres*) and Baird's Sandpipers (*C. bairdii*), they represented 98% of birds on the grid. Overall, 91% of birds on the grid foraged; the remainder loafed or preened between foraging bouts. We confined subsequent analyses to the 5 most abundant species and we included only foraging individuals.

Foraging ecology. Patterns of habitat use varied among the five species of shorebird (Fig. 2). Species differed in their use of (1) cobble and sand substrates (Fig. 2A; $G = 77.0$, df = 4, $P < 0.0001$); (2) foraging techniques (Fig. 2B; $G = 92.2$, df = 4, $P < 0.0001$); (3) wading vs. terrestrial habitats (Fig. 2C; $G = 63.4$, df = 4, $P < 0.001$); and (4) proximity to tide edge (Fig. 2D; $G = 113.5$, df = 4, $P < 0.001$). Overall, Least and Western sandpipers were most similar in foraging ecology and habitat use. Both species foraged close to the tide edge (81% and 94% of observations, respectively, occurred within 1 m of the aquatic-terrestrial edge) in sandy substrates (55% and 83% of observations, respectively). Of these two species, Western Sandpipers

TABLE 1.   Relative abundance of shorebird species observed on study grid between 27 July and 24 September 1991.

Species	Total	% Abundance	% Birds foraging
Least Sandpiper, *Calidris minutilla*	473	70.0	93
Western Sandpiper, *Calidris mauri*	137	20.0	96
Semipalmated Plover, *Charadrius semipalmatus*	41	6.0	49
Ruddy Turnstone, *Arenaria interpres*	14	2.1	93
Baird's Sandpiper, *Calidris bairdii*	10	1.5	100
Black Turnstone, *Arenaria melanocephala*	5	0.7	80

(54% observations >2 cm wading depth) tended to wade deeper than Least Sandpipers (27% observations >2 cm depth). Both species were very similar in their foraging behavior, predominantly extracting invertebrates from substrates using a multiple probe technique. Similar to Least and Western sandpipers, Baird's Sandpiper fed mostly in sandy substrates using the multiple probe technique, but they foraged at greater distances (90% of observations greater than 1 m) from the tide edge. Compared to calidridine sandpipers, Semipalmated Plovers and Ruddy Turnstones occupied terrestrial sites; they never waded and most individuals (58% and 62%, re-
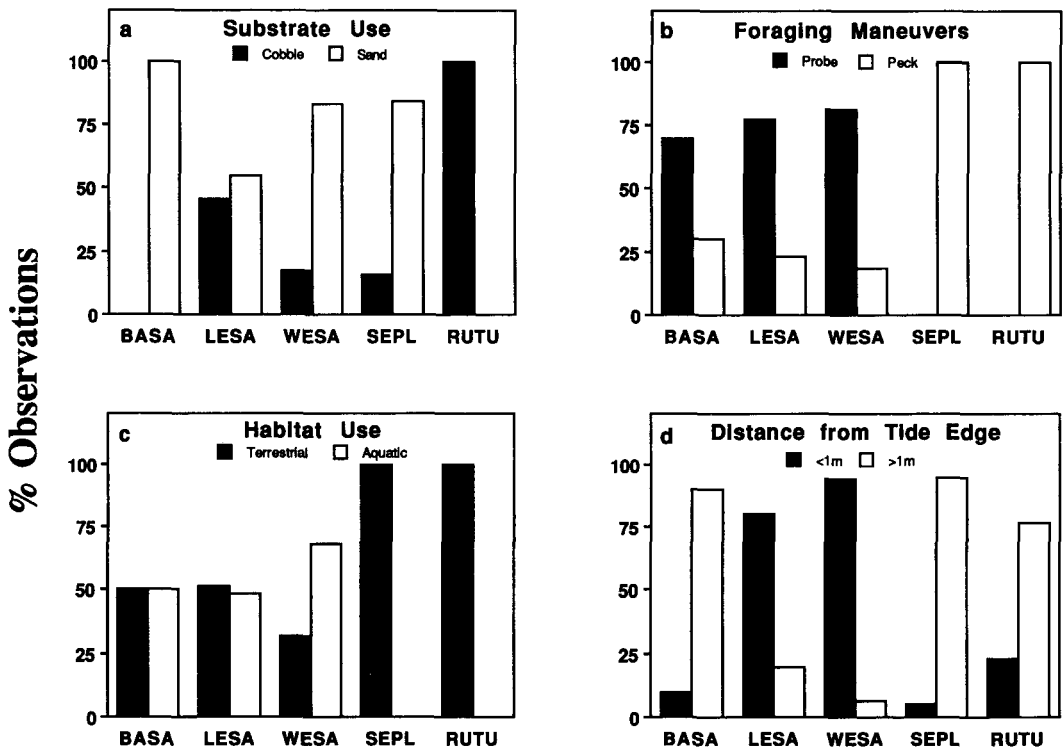
Shorebird Species

FIGURE 2.   Foraging ecology of the five most abundant shorebirds in the Mad River estuary portrayed as percent observations (*n* shown in Table 1) in which species: a) used sand or cobble substrates; b) pecked or probed for prey; c) foraged within habitats that were or were not covered by water; d) foraged >1 or <1 m from the tide edge. Species acronyms: BASA, Baird's Sandpiper; LESA, Least Sandpiper; WESA, Western Sandpiper; SEPL Semipalmated Plover; and RUTU, Ruddy Turnstone.
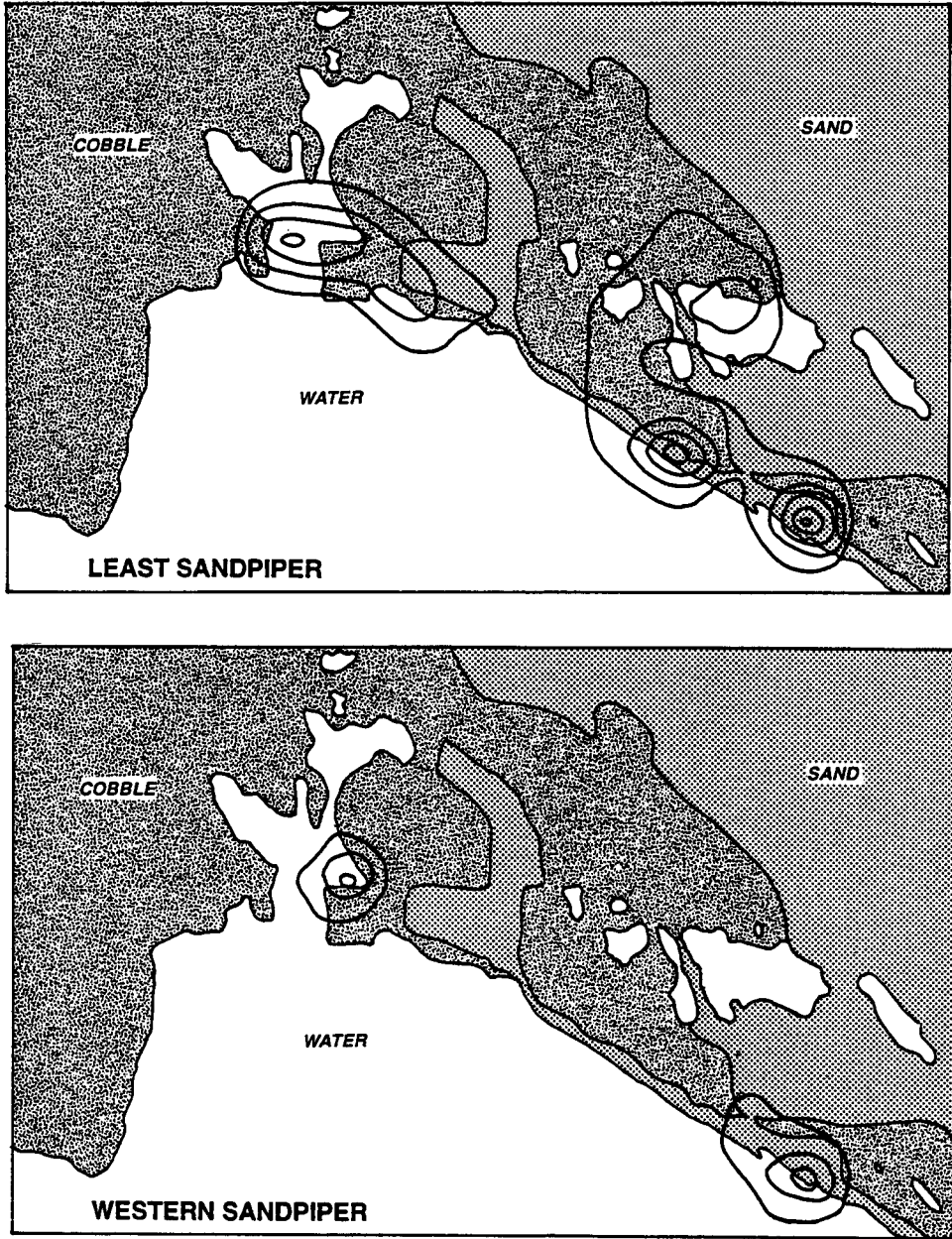
FIGURE 3.   Distribution and abundance of Least and Western sandpipers within the study area. Contour lines increase at intervals of one bird. Dimensions of study area are 25 × 40 m.

spectively) foraged >10 m from tide edge. Pecking characterized the foraging behavior of both species. Plovers used single-peck techniques in sand, whereas turnstones flipped over rocks and pecked at prey in cobble.

Spatial distribution of birds. All species, except the Semipalmated Plover, exhibited nonrandom, clumped distributions (s^2:$\bar{x} \gg$ 1; Fig. 3), but areas of highest density varied among taxa. Highest densities of Least (s^2:$\bar{x}$ = 21.7, t = 76.06, $P <$ 0.0001), Western (s^2:$\bar{x}$ = 17.6, t = 60.81, $P <$ 0.0001) and Baird's sandpipers (s^2:$\bar{x}$ = 1.7, t =
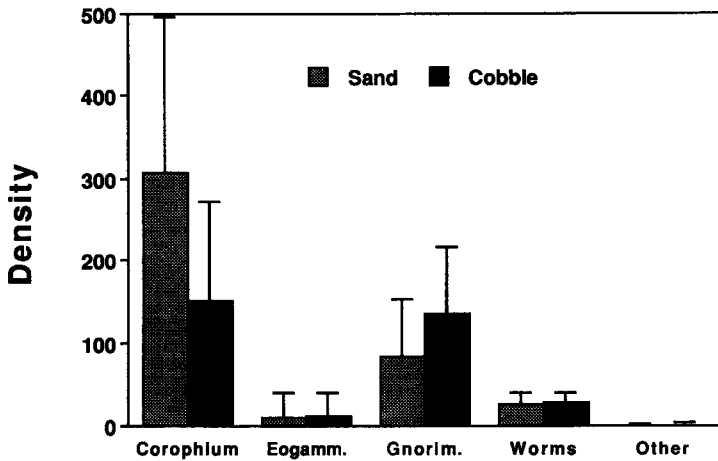
FIGURE 4.   Invertebrate abundance ($\bar{x} \pm$ SD) in sand ($n = 45$) and cobble ($n = 82$) substrates within the study area.

2.54, $P < 0.02$) occurred in areas adjacent to the tide edge or in shallow tidal pools with minimal water movement. By comparison, most Ruddy Turnstones ($s^2:\bar{x} = 1.8$, $t = 2.75$, $P < 0.01$) and Semipalmated Plovers ($s^2:\bar{x} = 1.2$, $t = 0.88$, $P > 0.20$) foraged in areas greater than 1 m from the tide edge.

Invertebrate abundance and distribution. For our analysis, we categorized invertebrates into one of five groups, including two species of amphipod (*Corophium* spp., *Eogammarus* spp.), an isopod (*Gnorimosphaeroma* spp.), marine worms (polychaetes and oligochaetes), and unidentified invertebrates. Invertebrate densities varied significantly among samples indicating highly variable, clumped spatial distributions (Fig. 4). Densities of the two most abundant invertebrates

varied significantly between sand and cobble substrates (Fig. 4). *Corophium* was twice as abundant in sand compared with cobble ($t = 5.02$, $P = 0.0001$), whereas *Gnorimosphaeroma* densities were higher in cobble than sand ($t = 3.55$, $P = 0.0006$). Densities of *Eogammarus,* marine worms, and other invertebrates were very low and did not differ between sand and cobble substrates ($P > 0.25$). Regression analyses, however, revealed no relationship between substrate index and invertebrate densities ($P > 0.05$).

Numerical relationship between birds and prey. When analyzed on a coarse scale (25 m²), prey densities explained 53% and 40% of variation in abundance of Least and Western sandpipers, respectively (Table 2, Fig. 3). For both species, most variation in bird abundance was attribut-

TABLE 2.   Relationship between shorebird abundance and invertebrate densities expressed as partial r^2 from stepwise forward regression.[a]

Invertebrate	Least Sandpiper		Western Sandpiper		All shorebirds	
	r^2	P	r^2	P	r^2	P
Corophium spp.	0.36	0.0007	0.31	0.0002	0.22	0.0001
Eogammarus sp.	—[b]		—		0.04	0.05
Gnorimosphaeroma spp.	0.05	0.14	—		—	
Marine worms	0.04	0.14	—		—	
Other invertebrates	0.07	0.09	0.10	0.06	—	
F		6.47		8.50		10.02
Total r^2	0.53	0.0012	0.40	0.0015	0.26	0.0001
df		4, 23		2, 25		3, 85

[a] Data for Least and Western sandpipers are based on total birds and average invertebrate densities within 25 m² grid sections ($n = 28$), whereas analysis of all shorebirds is derived from total shorebirds within 1 m of invertebrate core samples.
[b] Variable did not meet 0.5 significance level for entry into the model.

able to variation in the abundance of one invertebrate, *Corophium*. None of the other invertebrate taxa explained significant variation in abundance of Least and Western sandpipers. On a fine spatial scale (within 1 m of core sample), the relationship between shorebirds and prey remained significant (Table 2), but overall prey densities explained less variation (26%) in bird abundance. *Corophium* explained 22% of variation in shorebird abundance.

DISCUSSION

Our results demonstrate that shorebirds were not randomly distributed within microhabitats of the Mad River estuary. Foraging sandpipers aggregated in areas of sandy substrates adjacent to the tide edge, whereas Semipalmated Plovers and Ruddy Turnstones used drier sand and cobble substrates, respectively, more distant from the tide edge (Fig. 3). Moreover, variation in densities of the two most abundant species (Least and Western sandpipers) correlated positively with density of a single invertebrate, *Corophium* spp. (Fig. 5), which is known to be an important prey organism of many shorebirds (Bengston and Svensson 1968, Goss-Custard 1970, Hicklin and Smith 1984, Peer et al. 1986, Wilson 1990).

Many factors affect the distribution of shorebirds by influencing the distribution of their invertebrate prey, most notably variation in substrate, salinity and other physical features of the environment, which influence the abundance and availability of prey (Goss-Custard 1984) and selectivity of foraging birds for prey of different size classes (Sutherland 1982, Peer et al. 1986). Furthermore, these factors probably interact to influence the numerical response of shorebirds to prey.

Abiotic factors (e.g., salinity and substrate), which vary with spatial scale, strongly influence bird distributions through their impact on the distribution of prey organisms (Wolff 1969). Within our small study area (25 × 40 m) and short sampling period (63 days) it is unlikely that salinity varied enough to strongly influence variation in invertebrate abundance, which was substantial (Fig. 4). It is more likely that variation in invertebrate abundance obtained owing to substrate differences, which are known to strongly influence invertebrate abundance and availability to foraging shorebirds (Myers et al. 1980, Quammen 1982, Grant 1984).

Two species numerically dominated the Mad River invertebrate community and both exhibited strong substrate affinities (Fig. 4). *Corophium* spp., a burrow-dwelling amphipod, exhibited highest densities in sandy substrates, whereas highest densities of the isopod *Gnorimosphaeroma* occurred in cobble substrates. Highest densities of Calidridine sandpipers occurred along a narrow strip of habitat in close proximity to the tide edge (Figs. 2, 3). Approximately 75% of sandpipers probed for prey and most (96% of all sandpipers) did so in sandy substrates. Although we found it impossible to identify small prey organisms taken by shorebirds, it is noteworthy that we never observed birds capturing large prey (polychaete or oligochaete worms). Our observations of foraging birds strongly suggested that sandpipers used the multiple-probe maneuver to feed on a single prey organism; and, coupled with data on invertebrates, these observations suggest that sandpipers foraged almost exclusively on *Corophium* spp.

A meaningful understanding of the influence of prey on shorebird distribution necessitates distinguishing between prey abundance and availability (Goss-Custard 1984). If, as we argue, sandpipers foraged nearly exclusively on *Corophium*, then the concentration of shorebirds in sandy, edge habitats is likely influenced by an interaction between *Corophium* density and physical constraints on foraging birds imposed by the environment. Foraging shorebirds tend to avoid drier substrates (Prater 1972, Smith 1974, Goss-Custard 1977, Grant 1984); and experimental studies (Myers et al. 1980, Quammen 1982) have demonstrated that substrate texture influences the ability of a bird to penetrate the substrate when probing for prey, which results in birds spending less time in areas of coarse substrate. Furthermore, increased substrate wetness, owing to tidal inundation, probably affects prey availability in two ways: (1) it makes substrates easier to penetrate (Myers et al. 1980, Grant 1984); and (2) it increases invertebrate activity, rendering prey more susceptible to shorebird predators (Goss-Custard 1984). *Corophium* do not appear at the surface in dry areas of sand or mud, and it may be because of this that Redshank (*Tringa totanus*) avoid such areas (Goss-Custard 1970). Other species may respond similarly (Burger et al. 1977, Evans 1976, Prater 1972, Recher 1966).

Prey density alone is unlikely to account for all variation in bird density (Puttick 1984). Den-

TABLE 3. Studies demonstrating a positive numerical relationship between shorebird density and prey abundance, organized in order of decreasing spatial scale of study.

Shorebird species	Prey species	Source
Spatial scale: >1,000 m		
Haematopus ostralegus	Mytilus, Macoma, Cerastoderma, Anadara	a, b, c, d
Numenius arquata	Nereis, Macoma, Uca, Callinectes, Panopeus, fish	a, c, d
Limosa lapponica	Lanice	e
Pluvialis squatarola	Lanice	e
Tringa totanus	Corophium	e
Calidris pusilla	Corophium	f
Calidris alpina	Nereis, Hydrobia	a, c, e
Calidris canutus	Cerastoderma, Hydrobia, Macoma, Mytilus	a, c, e, g
Spatial scale: 1,000–100 m		
Haematopus ostralegus	Cerastoderma	e, h, i
Tringa totanus	Corophium, Nereis, Hydrobia	c, e
Numenius arquata	Polychaetes	e
Calidris canutus	Hydrobia	e
Calidris pusilla	Corophium	j
Spatial scale: 100–10 m		
Calidris pusilla	Corophium	f
Calidris alpina	Nereis	k
Spatial scale: <10 m		
Calidris minutilla	Corophium	l
Calidris mauri	Corophium	l
Spatial scale: <1 m		
Total shorebirds	Corophium	l

a) Wolff 1969, b) O'Connor and Brown 1977, c) Bryant 1979, d) Zwarts et al. 1990, e) Goss-Custard et al. 1977, f) Hicklin and Smith 1984, g) Prater 1972, h) Meire and Kuyken 1984, i) Sutherland 1982, j) Wilson 1990, k) Bengston and Svensson 1968, l) this study.

sities of Curlew Sandpipers (*Calidris ferruginea*) and Eurasian Oystercatchers (*Haematopus ostralegus*) increased with greater prey abundance, but at high prey densities bird numbers declined (Puttick 1984, Sutherland 1982). In both of these studies, an inverse correlation obtained between prey density and size; and birds aggregated in areas of high foraging profitability, where fewer, larger prey existed (Puttick 1984).

Corophium is known to be an important food item of several shorebirds (Table 3), especially on southward migration routes (e.g., Hicklin and Smith 1984). We did not distinguish between size classes of *Corophium,* but did note that very small individuals dominated some samples with the highest densities. It may be that the relatively weak relationship between sandpiper abundance and *Corophium* density obtained because birds selected areas where large-sized individuals occurred and did not forage in unprofitable areas

dominated by small prey. This speculation warrants further analysis, but Semipalmated Sandpipers (*Calidris pusilla*) do feed selectively on *Corophium* greater than 4 mm length (Peer et al. 1986).

Shorebird–prey distributions. Numerous studies (Table 3) have demonstrated positive numerical relationships between shorebirds and prey abundance or biomass, but the strength of the relationship varies among studies. In several studies conducted within large estuaries (e.g., Wolff 1969, Prater 1972, Goss-Custard et al. 1977, Bryant 1979, Hicklin and Smith 1984), shorebird densities correlated strongly with abundance of their principal prey species. For example, invertebrate densities explained 41–87% of variation in Oystercatcher, Eurasian Curlew (*Numenius arquata*), Redshank, Red Knot (*C. canutus*) and Dunlin (*C. alpina*) densities across 35 km of the Forth estuary, UK (Bryant

1979). Across 7 km of the Ythan estuary, Scotland, Redshank abundance correlated positively with *Corophium* densities (Goss-Custard 1970, 1977). Finally, Semipalmated Sandpiper abundance within the upper Bay of Fundy, Canada correlated positively with densities of *Corophium* (Hicklin and Smith 1984). These studies examined shorebird–prey associations within large estuaries on spatial scale ranging from several to 50 km.

By contrast, studies of shorebird–prey distributions conducted on finer spatial scales have not produced such strong numerical relationships (Table 3). For example, Wilson (1990) demonstrated a weak positive relationship between Semipalmated Sandpiper abundance and *Corophium* densities at stations spaced 200–300 m apart in the upper Bay of Fundy. Kelsey and Hassall (1989) studied Dunlin patch use on a 40 × 60 m site with appreciable variation in substrate texture and topography. They demonstrated that highest Dunlin densities occurred in wetter, low-lying habitats that supported lowest abundance of their principal prey organisms (oligochaete worms).

Our findings, therefore, are noteworthy because they extend knowledge of the positive numerical relationship between shorebird predators and their invertebrate prey to finer spatial scales than previously considered. Nevertheless, compared with estuary-wide studies, we demonstrated only weak relationships between bird abundance and invertebrate densities.

Spatial scale of analysis is important in interpretation of factors associated with bird distributions (Wiens 1989), an observation noted by researchers of shorebirds (Wilson 1990) and seabirds (Schneider and Duffy 1985). Patterns detected at large spatial scales may disappear upon finer scale analysis. For example, the strong numerical relationship ($r = 0.88$) between Semipalmated Sandpipers and *Corophium* among 10 sites in the upper Bay of Fundy (Hicklin and Smith 1984) disappeared when analyses were confined to a single site (Avonport; Wilson 1990). Furthermore, variation in physical features of the environment, which are known to strongly influence invertebrate distributions (Holland 1985), increase as one expands the spatial scale of analysis. As a result, one would expect variation in invertebrate densities across estuaries to exceed that found within sites. It also would follow that the abundance of shorebirds foraging on specific prey species would vary strongly.

We conclude that shorebirds often are distributed nonrandomly within estuaries in association with their invertebrate prey species at all spatial scales (Table 3). However, numerical relationships apparently vary with spatial scale of analysis (Wilson 1990), with models decreasing in predictive ability with finer scale resolution. The reasons for this require further study.

ACKNOWLEDGMENTS

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