The impact of foraging by sandpipers (Scolopacidae) on populations of invertebrates in the intertidal zone of Chomes Beach, Gulf of Nicoya, Costa Rica

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Foraging by sandpipers in the intertidal zone of Chomes Beach in Costa Rica affected populations of invertebrates upon which they fed during the 1986–1987 wintering period. Significant differences were found in the numbers of invertebrates inside and outside exclosures that were constructed on the mudflats where the sandpipers foraged. There was an inverse relationship between the numbers of crustacean- and bivalve-eating sandpipers and the differences in the numbers of crustaceans and bivalves found inside and outside the exclosures. Similarly, the abundances of *Uca* crabs varied inversely with the numbers of sandpipers. However, as with the other invertebrates, crab abundance did not diminish at the end of the season. Overall, no relationship was found between the total numbers of sandpipers foraging in the area and the differences in the total numbers of invertebrates found inside and outside the exclosures.

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Se determinó que el forrajeo de los correlimos en la zona de entremareas de la playa de Chomes, Costa Rica, afectó las poblaciones de invertebrados durante el periodo de invernación 1986–1987. Se encontró diferencias significativas en el número de invertebrados dentro y fuera de las áreas protegidas del forrajeo de los correlimos. Este mismo resultado se encontró al analizar el número de individuos de las especies de invertebrados más comunes del área, dentro y fuera de las áreas protegidas. Existe una relación inversa entre el número de correlimos comedores de crustaceos y bivalvos y las diferencias encontradas entre las áreas protegidas y fuera de ellas en número de individuos de estos de invertebrados. Sin embargo, no se rencontró relación entre el número total de correlimos que forrajearon en el área y la diferencia de invertebrados dentro y fuera de las áreas. La abundancia de cangrejos está relacionada inversemente con el número de correlimos que se alimentan de ellos. Sin embargo, al igual que con el resto de los invertebrados, no disminuye la abundancia al final de la época.

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Les habitudes alimentaires des Scolopacidés dans la zone intertidale de la plage Chomes au Costa Rica ont eu des répercussions sur les populations d'invertébrés qui leur ont servi de nourriture durant la période d'hivernage de 1986–1987. On a observé des différences significatives entre le nombre d'invertébrés à l'intérieur d'exclos érigés sur les slikkes où s'alimentent les Scolopacidés, d'une part, et à l'extérieur de ceux-ci, d'autre part. On a en effet découvert que le nombre de crustacés et de bivalves dénombrés à l'intérieur et à l'extérieur des exclos était inversement proportionnel au nombre de Scolopacidés s'en nourrissant. De même, l'abondance de crabes *Uca* variait en proportion inverse du nombre de Scolopacidés. Toutefois, comme pour les autres invertébrés, l'abondance de crabes n'a pas diminué à la fin de la saison. Globalement, on n'a pas trouvé de rapport entre le nombre total de Scolopacidés s'alimentant dans la région et le nombre total d'invertébrés se trouvant à l'intérieur et à l'extérieur des exclos.

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Introduction

After reproducing at high latitudes in the north, sandpipers migrate southward, where they concentrate along the coasts of Central and South America. There, they spend the overwintering period foraging on polychaetes and bivalves and a variety of other invertebrates (see Schneider 1983).

In several studies carried out at wintering sites in extra-tropical areas, a reduction in populations of the prey of sandpipers was found as a result of the birds' intense foraging activities. At the mouth of the Tees River, Evans *et al.* (1979) discovered a 90% reduction in harvests of *Hydrobia* and an 80% reduction in those of *Nereis* as a result of foraging by sandpipers. Such reductions have not been found in the tropics (Duffy, Atkins & Schneider 1981; Schneider 1983).

In Costa Rica, the mudflats along the Gulf of Nicoya support large populations of sandpipers. One such area is Chomes Beach, which is used as both a stop-over and wintering site (Stiles & Skutch 1989).

The main objective of this research was to determine whether foraging by the sandpipers that use Chomes Beach affected invertebrate populations and whether the availability of these food resources diminished over the wintering period.

Materials and methods

This research was undertaken from September 1986 to August 1987 in the intertidal zone between the Chomes and Coco inlets at Chomes Beach (10°N and 85°W) on the Pacific coast of Costa Rica (Figure 1). The study area (50 ha) had a soft mud substrate characterized by the presence of polychaete and Diopatra tubes typically adorned with bits of leaves and shells, which are abundant in the area. There were also some patches of sandy substrate. Above the tide line there was a small sandy beach that bordered a mangrove swamp consisting principally of *Laguncularia racemosa* and *Avicennia germinans.*

In order to determine the impact of foraging by sandpipers on invertebrate populations, three 25-m^2 portions of the intertidal area were enclosed, 100 m apart, at a distance of 50 m from the mangrove swamp. Wooden stakes, connected by nylon rope at heights of 5, 10, 15, 20 and 25 cm from the substrate, delineated each quadrat. These exclosures prevented sandpipers, but not other predators, such as fish, from entering those specific portions of mudflat.

Invertebrates were sampled every two weeks at low tide. During the first eight sampling periods, two random samples of mud were taken inside and outside each exclosure using a 10-cm-diameter core pushed to a depth of 15 cm. Beginning in January, a 5.5-cm-diameter core was used, and the number of samples increased to six inside and outside each exclosure. Each mud sample was placed in a plastic bag containing a solution of 10% formalin in sea water with Bengal red to preserve and tint the invertebrates. The samples were then passed through a 1-mm mesh sieve to separate organisms equal to or greater than that diameter and then placed in vials with 70% alcohol and subsequently identified.

The densities of crabs were determined by using ten 4-m^2 quadrats along each of three 100-m-long transects, 50 m apart and perpendicular to the edge of the swamp (Figure 1). Quadrats were placed every 10 m along each transect, and, after a three-minute wait, the crabs inside each quadrat were counted. Each count was undertaken at a distance of 6 m from the quadrat using 7 × 50 binoculars to avoid interfering with the crabs' activities.

Following each sampling period, I surveyed a 1-km-long transect parallel to the beach between the Chomes and Coco inlets to determine how many sandpipers were present.

Results

A total of 27 species of Charadriiformes was observed in the study area (Table 1). The Gull-billed Tern *Sterna nilotica* and the first 18 species listed in Table 1 all foraged there. Up to 14 species, totalling 713 individuals, were observed during a single count (Figure 2). Although the number of species remained relatively constant until the end of April, the numbers of birds present in the area began to decline as early as February and March. Numbers continued to decline until August 1987. Throughout that period, in 18 of 23 invertebrate samples, larger numbers of invertebrates were found inside the exclosures (Table 2, Figure 3).

In order to determine if there were significant differences between the numbers of different species of invertebrates in the exclosures and the control areas, the Wilcoxon Test was applied to the data (Siegal 1972). Using this test, separate analyses were done on samples taken during the wintering period and those taken during periods after most of the sandpipers had migrated to the breeding grounds.

The numbers of invertebrates were significantly larger inside the exclosures than outside ($W = 55$, $n = 23$, $p < 0.01$) (Figure 3A). The same was true for samples taken during the sandpiper wintering period, which runs from September to March ($W = 12$, $n = 13$, $p < 0.01$); in the samples taken during their absence from the area, from April to August, on the other hand, the differences were not significant ($W = 13.5$, $n = 10$, $p > 0.05$). Nevertheless, the resource was not depleted, as the numbers of invertebrates did not decline throughout the period (Figure 3).

The same results were found when analysing for differences in the numbers of polychaetes inside and outside the exclosures for (1) all samples ($W = 51$, $n = 23$, $p < 0.01$); (2) samples taken during the wintering period ($W = 16$, $n = 13$, $p < 0.05$); and (3) samples taken after the wintering period ($W = 11$, $n = 10$, $p > 0.05$) (see Figure 3). For bivalves, significant differences were found only in samples taken during the wintering period ($W = 17.5$, $n = 13$, $p < 0.05$); for crustaceans, no significant differences were found.

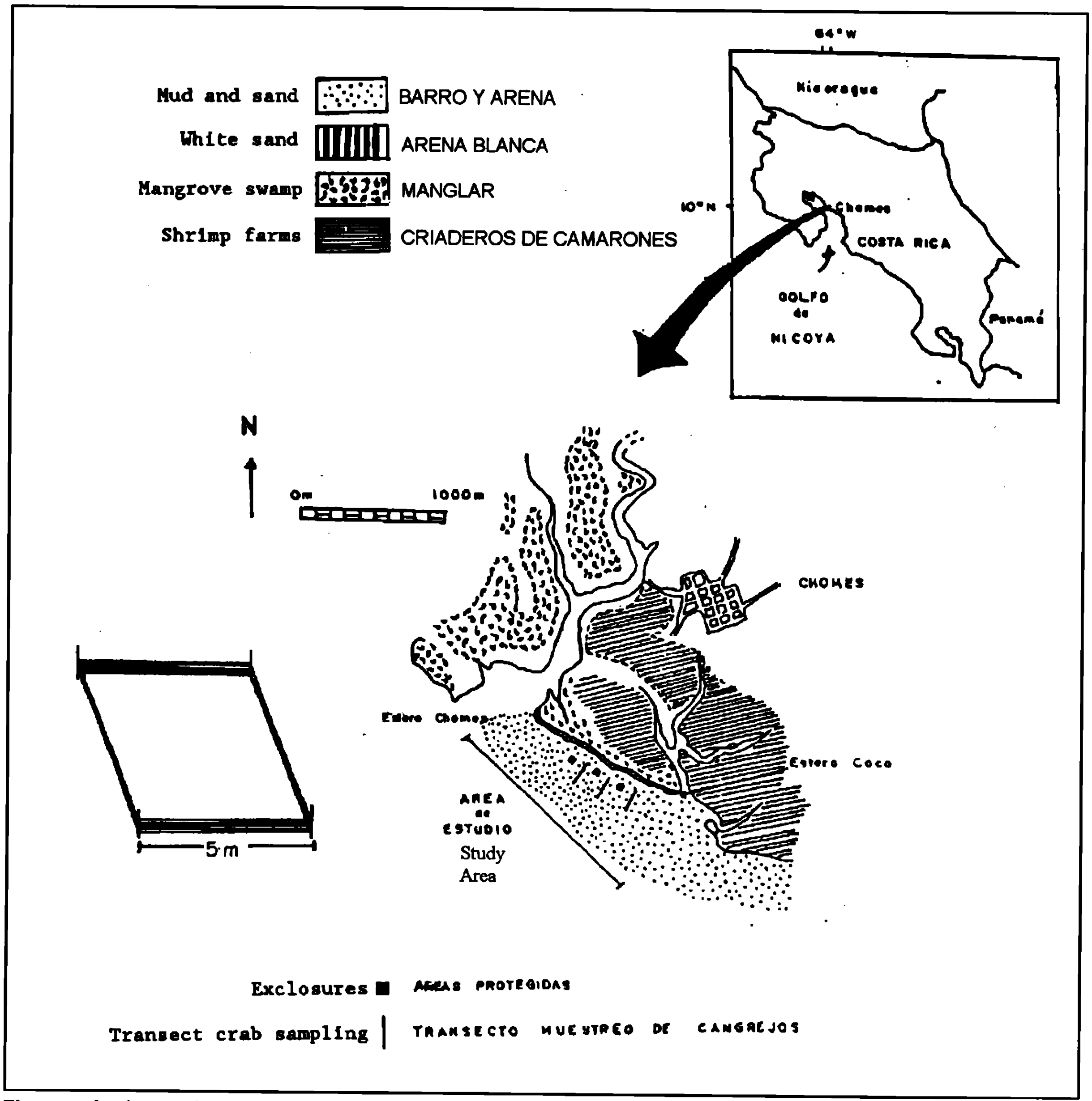

Figure 1. Study area, located in the intertidal zone of Chomes Beach, Gulf of Nicoya, Costa Rica.

Table 1. Charadriiformes sighted on Chomes Beach, Gulf of Nicoya, Costa Rica, between September 1986 and August 1987. Diet is shown in parentheses, where P = polychaete, C = crustacean, B = bivalve, F = fish and I = insects.

Haematopus palliatus (Temminck) (B)	*Numenius americanus* (Bechstein) (C,P)
Pluvialis squatarola (Linnaeus) (P)	*Limosa fedoa* (Linnaeus) (P)
Charadrius semipalmatus (Bonaparte) (P)	*Limnodromus griseus* (Gmelin) (P,B)
Charadrius wilsonia (Ord) (C)	*Himantopus mexicanus* (Muller) (C,I)
Tringa melanoleuca (Gmelin) (P)	*Larus atricilla* (Linnaeus) (F,B)
Tringa flavipes (Gmelin) (P)	*Larus pipixcan* (Wagler) (F)
Actitis macularia (Linnaeus) (C)	*Chlidonias niger* (Linnaeus) (F,C)
Catoptrophorus semipalmatus (Gmelin) (C,B)	*Sterna nilotica* (Gmelin) (C)
Arenaria interpres (Linnaeus) (B)	*Sterna maxima* (Boddaert) (F,C)
Calidris canutus (Linnaeus) (B)	*Sterna sandvicensis* (Latham) (F,C)
Calidris minutilla (Vieillot) (C,I)	*Sterna caspia* (Pallas) (F,C)
Calidris mauri (Cabanis) (C)	*Sterna antillarum* (Lesson) (F,C)
Calidris alba (Pallas) (C)	*Rynchops niger* (Linnaeus) (F,C)
Numenius phaeopus (Linnaeus) (C)	

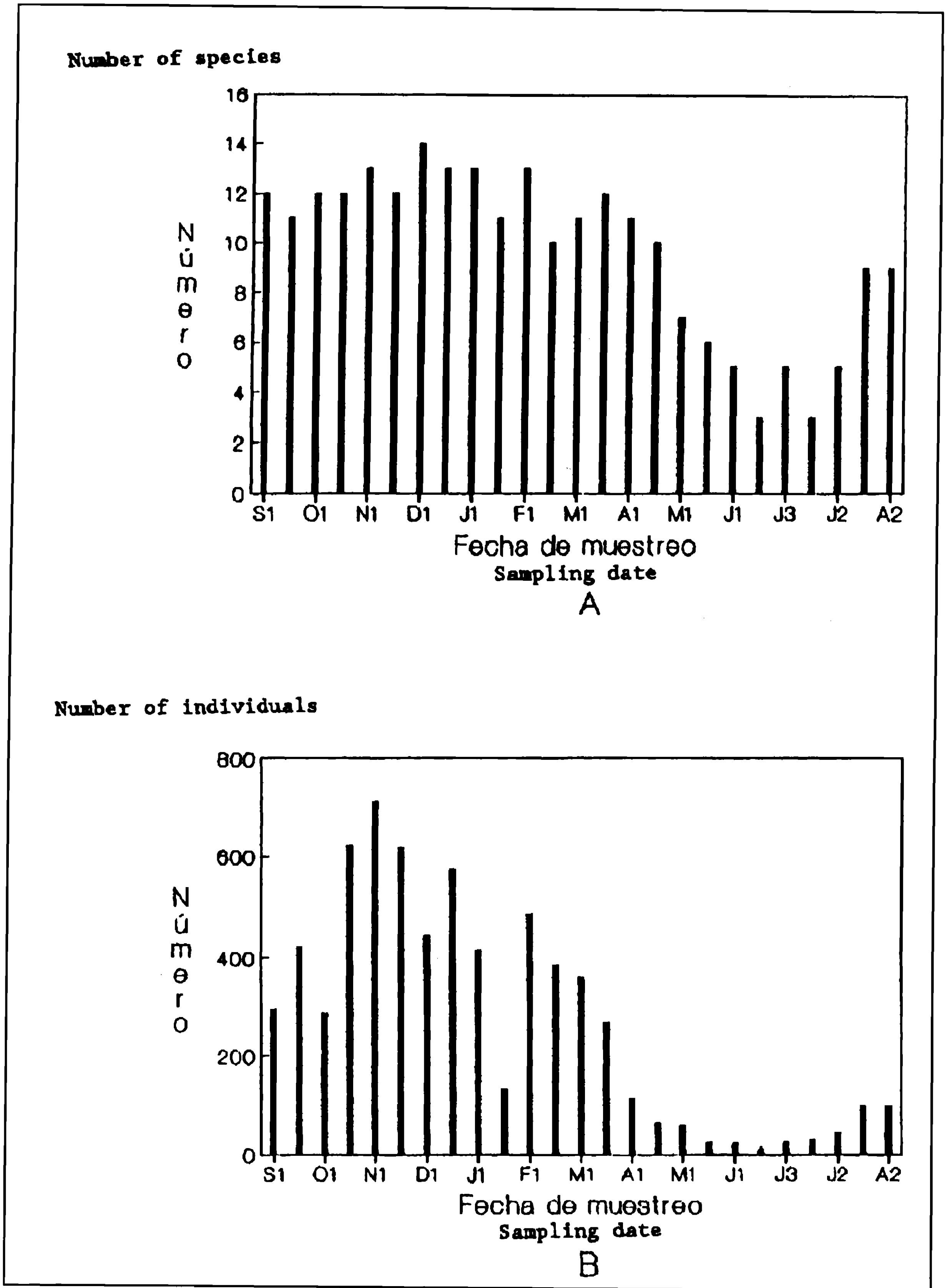

Figure 2. Number of species (A) and number of individuals (B) of sandpipers present during the 1986–1987 wintering period in Chomes Beach, Gulf of Nicoya, Costa Rica.

Table 2. Number of individuals from each invertebrate species found inside and outside exclosures during and after the wintering period, Chomes, Costa Rica. P = Polychaeta, B = bivalves, C = crustaceans, E = Echinodermata, Br = brachiopoda, F = filtered, AD = part of sediment, CA = carnivore, OM = omnivore.

	During wintering period		After wintering period	
	Inside	Outside	Inside	Outside
Owenia collaris (P–AD)	250	172	100	84
Notomastus hemipodus (P–AD)	67	54	18	9
Ophiophiolis geminata (E–AD)	53	40	41	34
Paraonidae sp. 1 (P–AD)	46	35	9	5
Armandia salvadoriana (P–AD)	42	34	10	13
Mediomastus californiensis (P–AD)	43	24	49	49
Nematoda	31	23	2	1
Phlytiderma phoebe (B–F)	31	18	14	26
Glottidia audebarti (Br–F)	22	25	8	15
Tharyx parvus (P–AD)	17	20	6	10
Polynoidae sp. 1 (P–AD)	17	19	27	17
Calyptraea mamillaris (C–F)	10	17	13	9
Nemertino sp. 1 (CA)	16	18	11	9
Hemipodus borealis (P–CA)	12	15	2	9
Pitar perfragilis (B–F)	13	13	26	21
Glycinde armigera (P–CA)	11	12	8	10
Sinelmis albini (P–AD)	15	7	8	8
Tellina tumbezensis (B–F)	16	6	16	14
Sipunculidae sp. 1	8	12	6	7
Linopherus spiralis (P–CA)	15	4	9	19
Pectinaria californiensis (P–AD)	12	6	2	2
Neanthes sp. 1 (P–CA)	11	6	8	2
Parapinnixa sp. (C–OM)	8	7	3	6
Mactra thracioides (B–F)	10	4	10	3
Encope estokessi (E–AD)	8	6	12	8
Tagelus bougeoisae (B–F)	7	7	12	7
Lumbrineris tetraura (P–AD)	4	9	7	6
Ceratonereis sp. (P–CA)	5	8	6	4
Tellina sp. (B–F)	11	2	6	10
Pinnixa valerii (C–OM)	7	6	3	10
Ancistrosyllis sp. (P–AD)	4	5	8	10
Tellidora burneti (B–F)	4	5	10	12
Corbula obesa (B–F)	8	0	7	15
Loimia medusa (P–AD)	5	2	11	5

The more common and abundant invertebrates also occurred in significantly higher numbers inside the exclosures during the wintering period ($z = -2.78$, $n = 32$, $p < 0.01$), whereas afterwards the differences were no longer significant ($z = -0.85$, $n = 32$, $p > 0.05$). The species that contributed most to these differences were the polychaetes *Owenia collaris*, *Mediomastus californiensis*, *Notomastus hemipodus* and *Linopherus spiralis*, the bivalve *Phlytimderma phoebe* and the starfish *Ophiophiolis geminata*, most of which represented the most abundant species. The birds *Limnodromus griseus*, *Charadrius semipalmatus* and *Pluvialis squatarola* fed on polychaetes; the stomach contents of several *L. griseus* collected in the area included large quantities of bivalve remains.

The Spearman Rank Correlation test was used to determine whether there was any relation between the differences in the numbers of invertebrates inside and outside the exclosures and the numbers of sandpipers present on the beach during the same period (P) and between the average numbers of birds sighted during the same period and during the previous period (P, P-1). This was done to correct for the effect of prior consumption and the delay in recovery of invertebrate populations.

The differences found in the numbers of invertebrates inside and outside the exclosures bore no relation to the numbers of birds foraging on the beach ($r_s = 0.17$ and $r_s = 0.10$, $n = 21$, $p > 0.05$, respectively, for P and P, P-1). Nor was there any relationship between the numbers of birds foraging on polychaetes and the differences in the numbers of these invertebrates between the two areas ($r_s = 0.25$ and $r_s = 0.21$, $n = 21$, $p > 0.05$, respectively, for P, P-1). However, an increase in the numbers of birds feeding on bivalves and crustaceans produced a greater increase in the differences between the numbers of both taxonomic groups, inside and

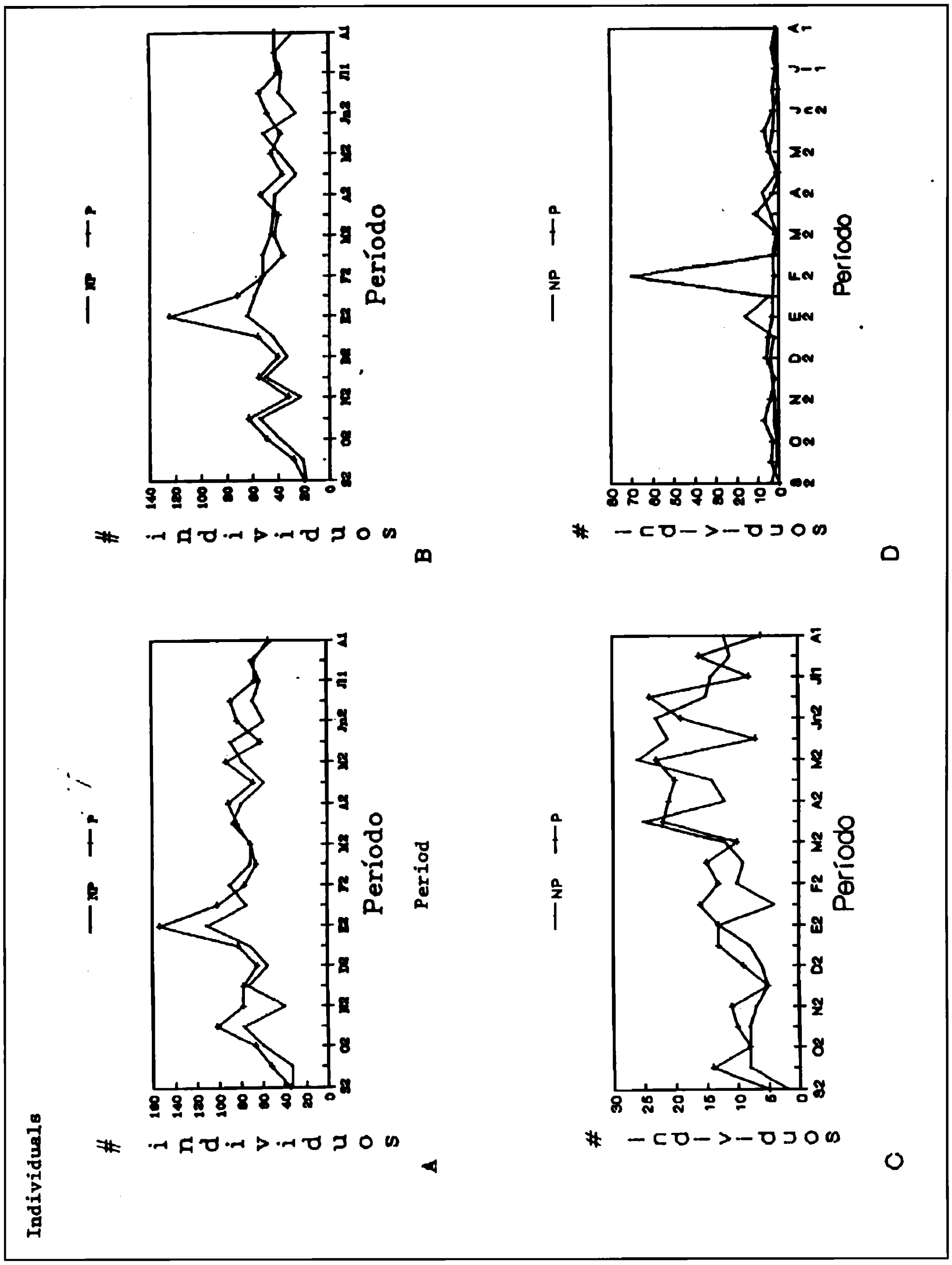

Figure 3. Number of invertebrates (A), polychaetes (B), bivalves (C) and crustaceans (D) present inside and outside exclosures in the intertidal zone of Chomes Beach, 1986–1987, Gulf of Nicoya, Costa Rica. P = exclosures; NP = control areas.

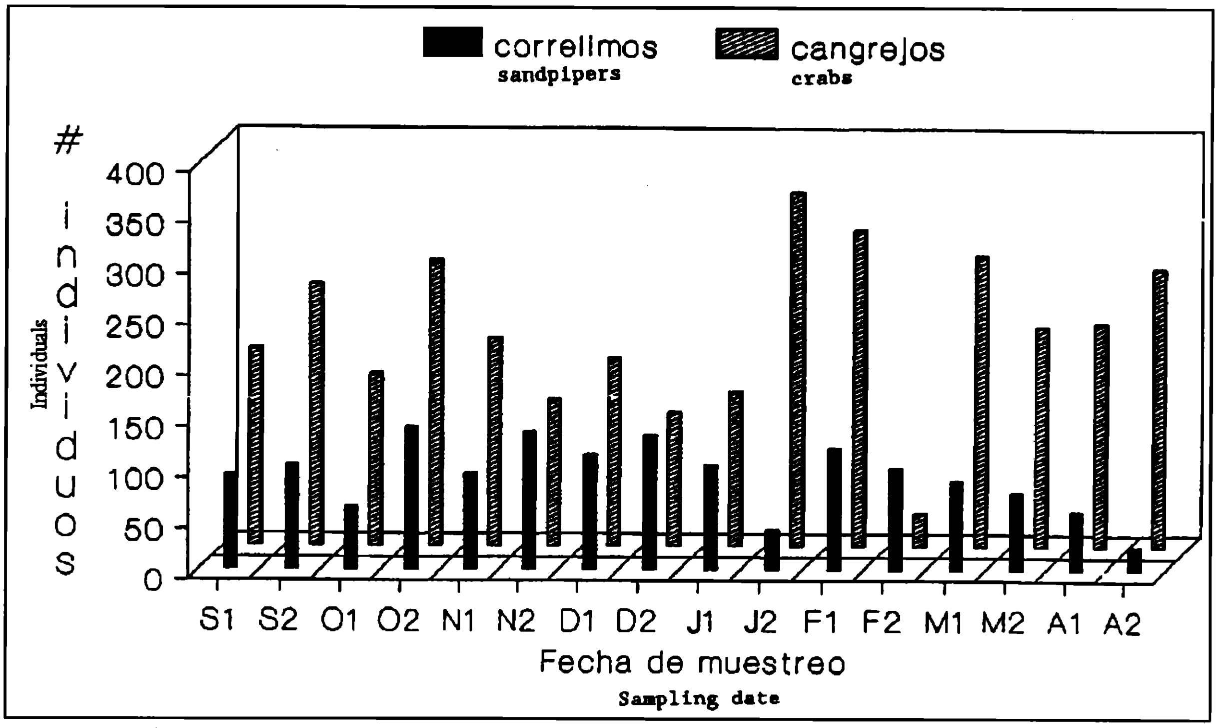

Figure 4. Number of crab-eating sandpipers and number of crabs present in each sample, Chomes.

outside the exclosures ($r = 0.38$, $p < 0.05$ and $r = 0.30$, $p > 0.05$; $r = 0.39$, $p < 0.05$ and $r = 0.38$, $p < 0.05$, for bivalves and crustaceans for periods P and P-1, respectively).

To determine whether there was any relation between foraging by *Numenius phaeopus*, *Catoptrophorus semipalmatus*, *Charadrius wilsonia*, *Actitis macularia* and *Sterna nilotica* and the crab populations upon which they fed, the Spearman Rank Correlation test was applied between the total numbers of individuals of all five species and the numbers of crabs sampled in each period (transect method). This was repeated with the average number of sandpipers present during the same period and the previous period.

Together, these birds caused a significant decrease in crab populations ($r_s = -0.61$, $n = 15$, $p < 0.05$; Figure 4). This effect was seen when we considered the average numbers of birds present during the same period and during the previous period. If we take into account the effect of these birds in each period, the same trend presents itself, although not to a significant degree ($r = -0.32$, $n = 16$, $p > 0.05$; Figure 3).

Most crabs caught by *Numenius phaeopus* and *Charadrius semipalmatus* were between 0.6 and 1.0 cm long. Crabs under 0.5 cm were infrequently captured by the birds.

Discussion

Foraging by sandpipers significantly affected the invertebrates upon which they fed. However, the foraging resources of these birds were not depleted in the latter months of the wintering period, as has been reported in other regions (Goss-Custard 1976, 1977, 1978, 1980; Evans 1979; Pienkowski 1981, 1983; Peer, Linkletter & Hicklin 1986). This may be attributable to the fact that breeding by invertebrates in the tropics is not confined to a particular season, as occurs in the extra-tropical areas, where most of these studies were undertaken.

Seasonality is present in the reproductive cycles of organisms in the tropics (Broom 1984; Cruz 1984; Vargas 1988), but different species breed at different times of the year (Vargas 1988). In a study carried out on a mudflat 2 km from the study area, Vargas (1988) found that organisms such as *Mediomastus californiensis* experienced breeding peaks during the dry season, whereas *Paraprionospio pinnata* had them during the rainy season; other species, such as the decapod *Pinnixa valerii*, showed peaks at breeding intervals of over a year. Hence, invertebrate species bred throughout the sandpipers' wintering period. This could compensate for depredation losses and may be one of the reasons why no decreases were found in the numbers of invertebrates at the end of the wintering period.

Crane (1975) reported that crab species of the genus *Uca*, which were abundant in the study area, reproduce throughout the year in the tropics. In a study of zooplankton done near the study area, Dittel (1989) found *Uca* crab larvae throughout the entire year.

Of the species of *Uca* reported in the study area, the sizes of the adults ranged between 0.53 and 2.5 cm (Crane 1975); individuals smaller than 0.6 cm were considered to be juveniles. *Numenius phaeopus* and *Charadrius semipalmatus* caught crabs that were usually between 0.6 and 1.0 cm long. This may explain why, although foraging by sandpipers affected crab populations, the latter were not in decline, because the sandpipers captured mainly adult individuals, thus allowing juveniles to remain in the population (see also Goss-Custard 1977, 1978; Hartwick & Blaylock 1979; Pienkowski 1983; Zwartz 1985, cited in Piersma 1987).

If food resources for sandpipers were not being depleted, why were there not more birds foraging in the area? One explanation might be the aggressive territorial behaviour of certain species, such as *Catoptrophorus semipalmatus*, *Numenius phaeopus* and *Charadrius wilsonia*. *Catoptrophorus semipalmatus* commonly defended areas of the beach against conspecifics and other species such as *Limnodromus griseus*. *Numenius phaeopus* and *Charadrius wilsonia* were less aggressive birds but frequently pursued or vocalized threats at conspecifics coming to forage or simply flying by.

It should be kept in mind that the exclosures used in this research prevented birds from foraging in specific areas but did not bar access to other predators, such as fish and macroinvertebrates, a problem present in the methodology used by other researchers. Sedimentation and stream flow problems that might have affected the results of the experiment (Quammen 1981) were absent as well.

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