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THE TROPHIC RELATIONSHIPS BETWEEN SHOREBIRDS AND THEIR PREY

ON BOLINAS LAGOON

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INTRODUCTION

The conservation and management of California's coastal wetland habitat requires a knowledge of the trophic relationships that tie estuarine organisms to one another. Aquatic birds are prominent members of the estuarine community; they are also particularly useful species to study because their conspicuous habits make them accessible both for research and interpretative purposes. About one third of the 60 uncommonly to abundantly (versus rarely) occurring aquatic bird species in our estuaries are shorebirds (Charadrii), a group that relies on the estuary for both food and resting sites during migratory, molting, and wintering periods.

The literature on shorebirds' diets is scattered primarily in short, incidental or anecdotal accounts. More rarely, comprehensive studies, that also measure the nature of the birds' food resource, have been undertaken but most of these have been done in Europe.

On Bolinas Lagoon, 37 species of shorebird have been found using the tidal flats during the past 12 years. Fourteen species occur for long enough periods and in great enough numbers to consume a significant number of prey (Page et al 1979). Twelve of these species and their substrate-dwelling prey are the subject of this report, which includes the following:

- 1) documentation of the distribution of the most common substrate-dwelling organisms in the lagoon,
- 2) determination of some of the tidal flat microhabitat characteristics correlative to local patchiness in the distribution of these organisms,

3) determination of the extent of seasonal variability in the number of these organisms,

4) documentation of the diets of 12 common shorebird species on the lagoon, and

5) determination of how spatial and seasonal variability in the abundance of the prey are reflected in the birds' diets.

DESCRIPTION OF STUDY AREA

Bolinas Lagoon is a shallow 570-hectare estuary 24 km northwest of San Francisco, California. High hills, marshy pastures, and the Seadrift sandspit surround Bolinas Lagoon except for a narrow opening to the ocean on the southwest side (Fig. 1). Pine Gulch Creek drains into the estuary year-round and is the main source of the estuary's fresh water. Kent Island is a 40-hectare island within the estuary. A large part of Kent Island and the Pine Gulch Creek delta are salt marsh where the chief plant species are Distichlis spicata, Salicornica virginica and Spartina foliosa. At mean low water about 70% of the estuary is composed of tidal flats which are divided by several channels (Ritter 1969). More detailed information on the physical characteristics of Bolinas Lagoon are available in Ritter (1969), Ritter and Brown (1973), and Berquist (1978).

We selected five areas within the tidal flat of the estuary (Fig. 1) for the most intensive study. The substrate of Area A was a very poorly sorted, very fine sand (Ritter 1969) containing considerable organic debris

such as twigs and leaves. Much of the high tide zone of this area was covered by a layer of sediment that was often dried and cracked into leathery plates. The high tide zone abutted a small salt marsh through which a fresh water stream ran year round; the low tide zone bordered a basin. Area B was similar to Area A except that a fresh water stream ran into it only during periods of heavy rain and the substrate ranged from fine to medium sand (Ritter 1969). The substrate of Area C was a well to moderately sorted fine sand (Ritter 1969) and lacked the organic debris of areas A and B. Unlike areas A and B, the high tide zone of Area C was pock-marked with the burrow openings of the ghost shrimp Callinassa californiensis and was not covered by hard dried plates of sediment. The high tide zone of Area C abutted the Kent Island salt marsh on one side and a channel on the other; the low tide zone bordered a small basin. Area D had a substrate of moderately sorted fine sand (Ritter 1969) and was bordered on two sides by channels and on a third by a basin. The high tide zone, lightly vegetated with a few sparse, scattered clumps of Spartina, in the center was less burrowed than in Area C. Area E differed markedly from the other areas. Its sediment ranged from medium sand through pebble. The pebble fraction contained numerous shell fragments and was largely in the low tide zone. The high tide zone was separated from the Kent Island sand beach by a shallow channel; the low tide zone bordered a main channel.

We distinguished microhabitats on these tidal flat areas, defined by elevation in the tidal zone and the water level in relation to the substrate surface. We defined the high tide zone of each area as the highest third of the area, the low tide zone as the lowest third, and the

mid tide zone as the area in between. In each zone, the tidal flat surface is marked by irregularly-shaped depressions 5 to 20 cm lower than the surrounding ground and from less than about 1 to 25 sq m in area. At low tide the centers of the depressions usually hold standing water (hereafter, submerged areas), the substrate on the perimeters is saturated to the surface (hereafter, saturated areas), and the surface of the surrounding higher ground is dry or slightly moist but emerged above the water table (hereafter, emerged areas).

METHODS

We divided the year into periods that correspond with climatic characteristics of the area and the nature of the shorebirds' annual cycle. Fall is defined as July through October,; winter as November through February, spring as March through May, and summer as the month of June. The fall period is characterized by a relatively warm dry season at Bolinas and it is the time when most shorebirds migrate and molt after breeding. The winter period corresponds with most of the rainy weather and the time of minimal migration and molt in shorebirds. The spring period heralds the return of warmer and drier weather to Bolinas and also a time of molt and migration in shorebirds. During June most birds have left the area for breeding grounds to the north and east and the number of shorebirds on Bolinas Lagoon is at a seasonal low.

As an estimate of the daytime availability of the tidal flat to shorebirds, we calculated the number of daylight hours during which the

tidal level was less than 1.4 m above mean low water, a level that approximates the lowest level of the salt marsh. This calculation was made for one day of every 3-day period of the 1973-74 season; we used the tidal charts to estimate the rate at which the water ebbed or flooded and the time at which the water level reached 1.4 m above mean low water.

Substrate cores were taken at low tide from each area to measure the relative abundance of small invertebrates, and from an invertebrate sampling plot (hereafter, ISP) to measure the seasonal abundance of some of these species. In 1973-74, Campbell Soup cans were used to take cores 9.8 cm deep and 6.6 cm in diameter. The cores were washed through sieves with 1 mm openings and the organisms retained were sorted and counted. Nine cores were taken from each microhabitat (with the exception of some very limited microhabitats) from all areas in June 1973 and from areas A, D, and E in December 1973. The ISP (280 x 20 m) lay along the southeast border of Area C and extended from the edge of the salt marsh to a basin in the low tide zone. Every month from July 1973 through May 1974, two cores were taken at random from each of 28 stations (10 x 20 m) along the length of the plot. From July 1972 until April 1975 we made monthly estimates of the algal coverage in each station of the ISP. To determine the effects of algae (beds of filamentous species, felt-like Vaucheria, and broad-bladed Ulva) on invertebrates, we compared the densities of selected invertebrates in cores from the substrate of a microhabitat lacking an algal covering with those from the same microhabitat having an algal covering. The alga and non-alga cores were taken from several microhabitats in areas A, C, and D during July and August in 1973 and 1974. The soup cans were pushed

through the algae into the underlying substrate to collect the cores. Organisms in each core were washed from the sediment and algae into screens with 1 mm openings, sorted, and counted.

Pellets, fecal material, and stomach-pumped samples were collected from shorebirds between July 1973 and January 1976. From Bolinas Lagoon we analyzed regurgitated pellets from Willets (Catoptrophorus semipalmatus) Long-billed Curlews (Numenius americanus), Black Turnstones (Arenaria interpres), Red Knots (Calidris canutus), and Sanderlings (Calidris alba), feces from Semipalmated Plovers (Charadrius semipalmatus), Black-bellied Plovers (Pluvialis squatarola), Godwits (Limosa fedoa), Red Knots, Sanderlings, Black Turnstones, Short-billed Dowitchers (Limnodromus griseus), and Long-billed Dowitchers (Limnodromus scolopaceus), and stomach-pumped samples from Short-billed Dowitchers, Dunlins (Calidris alpina), Western Sandpipers (Calidris mauri), and Least Sandpipers (Calidris minutilla) to identify their prey. In 1974 we also analyzed 20 stomach-pumped fall samples from Western Sandpipers at Limantour Estero, an estuary 21 km north of Bolinas Lagoon. Fresh pellets and feces were collected from locations where a group of roosting birds of a single species had just been flushed or from individuals after pellet regurgitation or defecation had been observed. These samples were preserved in alcohol for later analysis. Small sandpipers and dowitchers were trapped on the tidal flats during the day and in the Kent Island salt marsh at dusk to collect stomach-pumped samples. Samples were pumped from their stomachs by means of a plastic straw fixed to a disposable syringe. The straw (inside diameter of 3 mm) was guided down the bird's digestive

tract and into its stomach; a small volume of fresh water was forced into the stomach by pushing on the plunger of the syringe, then an equal volume of material was drawn into the straw by pulling back on the plunger. The straw was withdrawn from the digestive tract of the bird. Two to six draws were taken per bird and the contents from the straw were preserved in alcohol. We released the birds a few minutes after the samples had been taken.

All samples were examined at 25-X to 100-X under a dissecting microscope and a small fraction (usually six cover slips) of the well mixed matrix material in each fecal and stomach sample was examined for worm setae at 100-X to 1000-X under a compound microscope. Prey were identified by characteristic fragments and less often from entire specimens in the samples. Characteristic fragments of prey found in samples included claws and urosomes from amphipods and tanaidaceans, claws from decapods, hinges of pelecypods, setae and jaw parts from polychaetes, and ends of insect larvae and pupae. In recording the contents of each sample we estimated whether the organisms other than annelids contained in the sample were present in trace amounts (represented by fewer than three individuals) or in greater than trace amounts. It is often impossible to estimate the number of annelids present in a sample (unless the species have hard jaw parts), despite the fact that the matrix material of a sample may contain thousands of characteristic setae, all that remains after these soft-bodied organisms are quickly digested. The problem is compounded by the wide variation in the number of setae that occur on different species of annelids. We called an annelid's presence "trace" if we found one or fewer

setae of the species per cover slip and "primary" if we found more, although we recognize the problems of this method when comparing the occurrence of different prey species.

We followed Smith and Carlton (1975) for nomenclature of the tidal flat organisms. Many of the genera we report on are represented by a single species on Bolinas Lagoon; therefore, in referring to them in the text, after the first use of the full binomial we use generic names only unless we need to refer to particular species.

To determine the shorebirds' use of tidal flat microhabitat we made low tide censuses of the birds in each area in 1973-1974, counting the number of individuals of each species feeding in each of the microhabitats. Birds feeding in algae were counted separately.

To establish statistical significance of differences between means of invertebrate density, we used confidence limit tests, in which we reject the null hypothesis when the mean + or - 2 standard errors (to approximate the 90% confidence intervals of the means) do not overlap (Mood et al 1974).

RESULTS

PART I.

DISTRIBUTION OF THE TIDAL FLAT ORGANISMS

The following accounts briefly describe the distribution of the most abundant invertebrate species and species groups found in our June 1973 to May 1974 sampling of the ISP, the June 1973 sampling of areas A, B, C, D, and E, the December 1973 sampling of areas A, D, and E, and the alga samples taken from June to early August 1973 and 1974. In many cases there is more information about individual species in the inter-area and seasonal variability sections that follow the accounts. The accounts also identify species or species groups that were not adequately sampled by our core or screen sizes or in our sampling areas. For these organisms, we provide observations from other areas or information we obtained by searching our sampling sites for specific species.

ANTHOZOANS

The only anenome we found on the tidal flat is Nematostella vectensis. It is discussed below in the sections on inter-area and seasonal variability. Anenomes have no hard parts that would resist digestion, were they taken by birds.

NEMERTEANS

We found at least six species of nemerteans in our cores, including Lineus ruber in areas A, B, C, and D, cf. Micrura alaskensis in areas B, C, D, and E, cf. Carinoma mutabilis and an unidentified species in areas D and

E, Paranemertes peregrina in area D, and another unidentified species in area E. The only hard parts on nemerteans are the needle-like proboscideal stylets, which are neither large enough nor distinctive enough to be recognizable remains in the bird's food samples.

ANNELIDS

This category, used in many of our tables and figures, includes oligochaetes and polychaetes; polychaetes, however, were far more abundant than oligochaetes in our cores.

Oligochaetes

Like most marine oligochaetes, those in Bolinas Lagoon are minute and fragile and were not consistently retained in our sieves; therefore, we felt that the number in our samples did not provide a reliable estimate of their relative abundance in the different sample sets. We found them in the cores from the muddiest (Area A) to intermediate substrate types (Area C, ISP) suggesting they were to be most abundant in the finest sediments. West coast marine oligochaetes are a poorly known group and we did not specifically identify those retained in our samples. In winter shorebirds on Bolinas Lagoon retreat to upland habitat during prolonged periods of high tide and rain, so oligochaetes found in dietary samples in that period could have been captured in upland areas as well as on the lagoon.

Errant Polychaetes

The Phyllodocid Eteone spp. occurred sparsely in areas C and E in fall and in areas A and C in winter. From the microhabitats in which it was most common, saturated and submerged substrates in the high tide zones of areas A and C in winter, its density was only 1.6/100 sq. cm (se = 1.1/100 sq. cm). In fall, we found Eteone in the low saturated flats of Area C and in pools in the high tide clean sand of Area E, leading us to suspect that we were finding at least two species.

Nereids taken by shorebirds were not well represented in our cores. From 18 cores taken in brackish channels through Area A we found 2.3 Neanthes limnicola/100 sq. cm (se = 1.1/100 sq. cm). Single unidentified nereids were taken from the low tide zone cores of Area E in fall and Area D in winter. We identified a single specimen of Nereis vexillosa from the tidal flats of southeast Kent Island. Although we only detected a few Platynereis bicanaliculata in our alga-covered cores, it is taken fairly commonly by some shorebirds. Individuals of this species inhabit mucoid tubes on algae and spawn as a free-swimming epitoke, mostly in May, June, and August (Morris et al 1980); in both forms this species would be vulnerable to shorebird predators.

Glycinde sp., the only goniadid found in our cores, occurred in areas C, D, and E. It reached its highest density in alga-covered cores from high emerged microhabitat (mean = 3.2/100 sq. cm, se = 1.0/100 sq cm) of Area E.

The few Nephtys caecoides, found in Area D in June and December and

Area E in December, were the only representatives of Nephtyidae in our cores. This active worm may have been underestimated since it can move rapidly through the sandy substrate it inhabits and may have responded to our activities when we took the cores by moving away.

The lumbrinerid Lumbrineris zonata was the most abundant polychaete in intermediate to sandy substrate (areas C, D, and E). It occurred at its highest density (mean = 37.0/100 sq. cm, se = 6.3/100 sq cm) in saturated mid tide microhabitat of Area D in June. In the ISP we found 136 to 187 individuals/month from August through February, but only 90 to 124 individuals/month from March through July. It was absent from areas A and B in fall but we found a single specimen in Area A in winter cores.

Scoloplos acmaceps, the only orbinid in our cores, occurred in areas B, C, D, and E in June and area D in December. It was most common in area C where it reached a density of 5.5/100 sq. cm (se = 1.6/100 sq cm) in submerged mid tide areas.

Sedentary Polychaetes

We found seven species of Spionidae in our cores. Five species of the genera Boccardia, Polydora, and Pseudopolydora occurred in our cores, but we did not separate them at the time we sorted the organisms; they are considered together as Polydorids in our results. In June 1974 we made a cursory examination of spionids from the five areas we sampled in 1973. We found Boccardia proboscidea in the high tide zones of areas A, B, and D, Polydora brachycephala in the clean sand of Area E, Polydora nuchalis in

all five areas, Polydora socialis in the mid and low tide zones of areas C and D, and Pseudopolydora kemp in areas A, B, and C. Another species of Boccardia, B. hamata, did not occur in our cores but was taken by some species of shorebirds (see below). Scololepis squamatus occurred in our cores of Area E in June and December. Streblospio benedicti occurred in our cores of areas A, B, and C. It was most abundant in the high submerged microhabitat of Area A in December (mean = 29.2/100 sq. cm, se = 16.6/100 sq. cm). In the ISP it was clearly more abundant between December and April, when we found 65 to 158 individuals per month in our cores, than between May and November, when we found 8 to 39 individuals per month.

Two Opheliidae were found in our cores. Armandia acuta occurred in December samples from areas D and E and from September through February in the ISP. In December, we found a mean of 5.2/100 (se = 2.0) sq cm in low saturated microhabitat of Area D and 2.0/100 (se = 1.6) sq cm in mid submerged microhabitat of Area E. The occurrence of Armandia in the ISP was very seasonal: in September we found a total of 1, in October, 2, in November, 91, in December, 49, in January, 22, in February, 18, and in all other months, 0 individuals. Ophelia assimilis was found only in the low tide zone of Area E in both June and December.

We found four species of Capitellidae in our samples. In June Capitella capitata was found in all areas, but in much higher densities in areas A and B (mean = 65.8/100 sq. cm, se = 12.6/100 sq. cm in mid tide saturated Area A; mean = 31.8/100 sq. cm, se = 9.4/100 sq. cm in high tide submerged Area B) than in the other areas. Only two Heteromastus filiformis were found, both in Area A in June. Notomastus tenuis was found

in areas C, D, and E in June and in areas D and E in December. Mediomastus californiensis was found in all areas in June and in areas D and E in December.

We found very few Axiiothella rubrocincta (Maldanidae) in our samples: in high submerged Area D (mean = 1.3/100 sq. cm, se = 0.7/100 sq. cm) and in alga-covered low emerged Area C (mean = 0.3/100, se = 0.3/100 sq. cm).

TANAIDACEANS

Leptochelia dubia was the only tanaidacean found in our samples in 1973-1974 and its distribution is discussed below in the general section on invertebrate distribution.

AMPHIPODS

We divided the amphipods we found into alga-dwelling, tube-dwelling, and sand-dwelling species.

Alga-dwellers include Allorchestes angusta, Ampithoe lacertosa, Ampithoe valida, Anisogammarus confervicolus, and Anisogammarus pugettensis. Allorchestes was the most abundant alga-dwelling amphipod in all samples except those from Area A, where Ampithoe were the most abundant and Anisogammarus second most abundant alga-dwelling amphipod. We identified Ampithoe lacertosa from Ulva in areas D and E, Ampithoe valida from Ulva in areas A, C, D, and E, Anisogammarus confervicolus from Ulva in Area A, and Anisogammarus pugettensis from Ulva in areas A, D, and

E and filamentous algae in Area C; we did not distinguish beyond genera however, when we took the core samples.

Tube-dwellers include Ampelisca milleri, all Corophium with fused urosomes (these probably included C. uenoi, C. insidiosum, and C. acherusicum) C. stimpsoni, C. spinicorne, and Grandidierella japonica. Ampelisca milleri occurred primarily in the areas of finer sediment (A and B) in June. Relatively high densities occurred in Area A low submerged microhabitat (mean = 50.3, se = 22.4/100 sq. cm), and in Area B low submerged (mean = 58.1, se = 5.1/100 sq. cm) and low emerged microhabitat (mean = 57.4, se = 3.7/100 sq. cm). Fused Corophium were the most widespread and abundant tube-dwelling amphipods we sampled. Like other tube-dwelling amphipods, they reached peak abundance in the summer and early fall months. C. stimpsoni occurred in areas A, B, C, and E, but most abundantly in areas B and C. It is an organism of the low tide zone; 97% of the 584 C. stimpsoni found in the ISP occurred in the lowest 50 m of the 280 m long plot. C. spinicorne was found only in areas A and B, where it occurred in the mouths of fresh water channels that emptied into the high tide zone. Grandidierella occurred in all areas but reached peak densities in filamentous algal cores from the mid saturated microhabitat of the Area A June sample (mean = 63.8, se = 17.1/100 sq. cm). It is a low tide organism; 85% of the 183 Grandidierella found in the ISP occurred in the lower half of the plot.

In the category of sand-dwelling amphipods we included Eohaustorius sp. and the less common Paraphoxus cf. epistomus, both found only in Area E, Orchestoidea spp. of the high sand beach of Kent Island (Area G of Fig.

1), and Orchestia traskiana from the Kent Island salt marsh.

DECAPODS

Decapods are generally too large and widespread on the tidal flat to be suitably sampled by our small invertebrate cores. Burrow openings of some species are conspicuous on the tidal flat surface and the organisms' presence can be inferred from fecal pellets left at these openings. Other species occur under or in objects on the tidal flat. Information on decapod distribution obtained in our samples is augmented by our general observations of their presence.

We found three anomurans on the tidal flat. The blue mud shrimp Upogebia pugettensis did not occur in our samples but, by digging, we found it in burrows throughout the lagoon at the edge of low tide channels. We also saw Long-billed Curlews capture them in these areas on numerous occasions (Stenzel et al 1976). The ghost shrimp Callinassa californiensis was found occasionally in our cores from the ISP. Most occurred in high tide areas but one was also found at the lower end of the plot. Their abundant burrows pock-mark the high and mid tide zone of the sand-mud areas in the central lagoon. The hermit crab Pagurus hirsutiusculus inhabits abandoned snail shells washed into the mouth of the lagoon and deposited in Area E.

The four brachyurans we found most commonly in the intertidal zone included Pinnixa longipes, Hemigrapsus oregonensis, H. nudus, and Pachygrapsus crassipes. Pinnixa, a commensal in the tubes of the worm

Axiiothella, was found sparingly in areas C and D in June. In Area C a single crab was found in a low emerged alga-covered area. In Area D we found two in low submerged and one each in high saturated, high submerged, and mid saturated microhabitats. We found Hemigrapsus oregonensis in all areas and microhabitats on the tidal flat that we searched. In the high, muddy areas of the lagoon they hide under leathery plates of mud; in sandy Area E and along the rip-rapped eastern shoreline of the lagoon they hide under cobbles and small rocks. On the rest of the tidal flat, and along channels in the salt marsh, they live in burrows in the substrate. H. nudus can be found along the perimeter of the lagoon where angular stones have been deposited for rip-rap. Pachygrapsus lives in burrows in the salt marsh and along salt marsh channels of Kent Island where they were numerous and conspicuously active after dark.

INSECTS

The insects obtained in our cores included adults and immature stages of the beetle Heterocerus sp. and larvae and pupae of several species of flies that lay their eggs in emerged areas of the high tide zone of areas of fine to intermediate sediment.

On Bolinas Lagoon Heterocerus is a beetle of the salt marsh and is rarely found on the tidal flat far from the edge of the marsh. In the ISP all Heterocerus occurred in the highest 20 m of the 280 m long plot; we found 3 in fall, 1 in winter, and 15 in spring.

We found five species of dipteran larvae and pupae. One species each

of Anthomyiidae and Ephydriidae were found in areas A, B, C, and D. We found a species of Ceratopogonidae only in area A and a species of Dolichopodidae in areas A and C. A second species of Ephydriidae was found in areas A, B, C, and D and around the Pine Gulch Creek delta.

GASTROPODS

Snails occupied limited intertidal microhabitats on the lagoon. Cerithidea californica were locally abundant in submerged areas in and near the edge of the salt marsh from Area A to the southeast end of Kent Island. Littorina scutulata were found on rocks, pilings, and drift in the high tide zone and in the salt marsh. Lacuna marmorata occurred in areas D and E on filamentous algae, Enteromorpha linza, and on Ulva. We found Ovatella myosotis in the Kent Island salt marsh and on the rip-rap along the eastern edge of the lagoon. Olivella biplicata occurred only in Area E, where we found it occasionally on clean medium sand in June.

BIVALVES

Bivalves were found in several situations on the lagoon tidal flat. Mytilus edulis were attached to pilings, stakes, snags, and debris on the tidal flat. Several species of clams live on or near the surface of the tidal flats and are commonly found at a size range acceptable to shorebirds as prey.

Small species of venerid clams, occurring from the finest sediments

on the lagoon to the muddy sands of Area D, were more abundant in the intertidal zone in the fall than the winter and spring periods. One of these, Gemma gemma is probably the most abundant clam on the lagoon. It occurs from areas A to D, mostly in the high and mid tide zone. We found it at highest densities in June in mid emerged microhabitats of the north end basin where it reached a mean density of 445.9/100 sq. cm (se = 61.0) in Area A and 436.0/100 sq. cm (se = 76.2) in Area B. In sandier areas C and D it occurred at much lower densities and was more abundant in saturated and submerged than in emerged microhabitats. Its highest mean densities in Area C were 81.8/100 sq. cm (se = 10.8) in mid saturated and 65.6/100 sq. cm (se = 27.6) in mid submerged microhabitats and in Area D 13.3/100 sq. cm (se = 8.3) in high submerged microhabitat. One or more species of Transennella also occurred in our area B, C, and D samples, but lower in the tidal zone than Gemma. Only one individual, in low emerged microhabitat, was found in each of areas B and C. In Area D Transennella was found in the mid and low tide zone and reached its peak density in mid saturated microhabitat in June (mean = 35.4/100 sq. cm, se = 8.6/100 sq. cm).

Other clam species were found uncommonly in our samples but could be found by digging deeper than our core depth. Some of these species grow to sizes larger than can be taken by shorebirds but smaller individuals (or their siphons) may be eaten by the birds. Cryptomya californica projects its siphon into the burrows of Callianassa and Upogebia, and its distribution, therefore, parallels those species. It is also reported to use the burrows of the echiuran worm Urechis caupo, a deep burrowing

species of low and subtidal levels that is also reported from Bolinas Lagoon (Morris et al 1980). We found Macoma nasuta in submerged areas on the east side of Kent Island. M. secta occurred near Area D, in slightly sandier areas than those inhabited by M. nasuta. The cockles Clinocardium nuttallii and Protothaca staminea and the clams Tressus nuttallii and Saxidomus nuttallii were species of sandy and cobbly areas near and in areas D and E. The latter two species often occurred in clams beds largely made up of one species.

HOLOTHUROIDEANS

Leptosynapta albicans was the only sea cucumber we found in the estuary. It only occurred in Area E and its distribution is described below in the general sections on inter-area and seasonal variation.

SPATIAL AND TEMPORAL DISTRIBUTION OF TIDAL FLAT ORGANISMS

A number of factors determine the distribution of the fauna on a tidal flat. Substrate texture (particle size, shape, and arrangement), salinity, and concentration of pollutants are recognized as some of the important factors affecting the distributions of benthic fauna (Carriker 1967, Nichols 1973). Also, each organism's ability to resist desiccation determines its distribution in the intertidal zone. Factors that affect the level of the water table when the tide is out, such as the porosity of the sediments, can alter an animal's distribution within the intertidal zone; only when the substrate is uniform throughout the intertidal zone,

will an organism's distribution be directly related tidal level (Day 1967). Consequently, irregularities on the substrate surface, such as pools, affect the distribution of the infauna. The five tidal flat areas we sampled on Bolinas Lagoon varied with respect to at least salinity and sediment texture. Other differences in the physical properties of each of the five areas, and in microhabitat therein, are apparent in even a casual inspection. These differences provide a potential for invertebrate segregation that are of particular interest to us since foraging shorebirds also segregate in relation to the water's edge.

Inter-Area Variability

Both the general types of invertebrates and the species in our samples varied considerably among different areas of the lagoon. Generally, the relative abundance of the anthozoan Nematostella and bivalves decreased from the finest to the coarser sediments while that of the tanaidacean Leptochelia increased (Table 1). The composition of the organisms found in Area E differed markedly from that in other areas. Sand-dwelling amphipods and Leptosynapta occurred only in Area E while insects and bivalves were absent only in Area E (Table 1). In June nemerteans and the relatively important groups, annelids and tube-dwelling amphipods, were of similar relative abundance in all the areas despite a change in species composition between areas. Alga-dwelling amphipods were clearly very uncommon in all non-alga-covered microhabitats in June. A more detailed description of the infauna of each area in June follows.

Bivalves were the most abundant organisms, with tube-dwelling amphipods and annelids next most numerous in Area A, our sampling plot with the finest sediment (Table 2). All bivalves in the cores were Gemma; they reached their peak density, averaging 152.6 per core (s.e. = 20.9) in mid emerged areas where they were significantly more abundant than in any other microhabitat (Table 2). Tube-dwelling amphipods comprised fused Corophium, primarily in the high and mid tide zones, and Ampelisca and Grandidierella primarily in the mid and low tide zones (Table 3). Annelids occurred in all microhabitats sampled but at a significantly higher mean density in mid saturated than any of the other microhabitats (Table 2). Polydorids were the most numerous annelids found in the high tide zone and in the mid submerged microhabitat, Capitella was the most numerous annelid in mid emerged and saturated microhabitat, and Streblospio was the most numerous in the low tide zone. Mean densities of other organisms and total organisms are given in Table 2. "Other" organisms were both Cerithidea.

Brackish mouths of fresh-water creeks in Area A provided an additional microhabitat that we sampled but did not include in Table 2. Annelids, including Neanthes, polydorids, Streblospio, and Capitella, and tube-dwelling amphipods, including fused Corophium, C. stimpsoni, C. spinicorne, Grandidierella, and Ampelisca, were the only organisms found in 18 cores taken from the creek mouths. The mean density of annelids per core (mean = 3.3, se = 0.6) was significantly less than that in nearby high submerged areas not fed by fresh water creeks; however, the mean number of tube-dwelling amphipods in the creek mouths (mean = 5.2, se = 1.4) was not significantly different from that in nearby high submerged areas. We found

Neanthes (mean = 0.8, se = 0.4 per core) and C. spinicorne (mean = 0.6, se = 0.3 per core) only in the creek mouths but the other species found in the creek mouths occurred in other microhabitats of Area A.

Area B, where sand intermixed with fine mud in some locations, was similar to Area A in the abundance of bivalves in the mid tide zone and tube-dwelling amphipods in the low submerged microhabitat. The mean density of bivalves in the mid emerged microhabitat was significantly higher than that of any other microhabitat in Area B (Table 4). All bivalves found in Area B were Gemma, except for one Transennella found in low submerged microhabitat. Tube-dwelling amphipods comprised fused Corophium, C. stimpsoni, C. spinicorne, Grandidierella, and Ampelisca. Fused Corophium occurred primarily in high submerged microhabitat, C. stimpsoni, only in the low tide zone, C. spinicorne, infrequently in low emerged microhabitat, Grandidierella, primarily in mid and low submerged microhabitats, and Ampelisca, primarily in the low tide zone. Annelids comprised polydorids, primarily in the high tide zone and in emerged microhabitats, Mediomastus in mid submerged microhabitat, Streblospio and Scoloplos, in the low tide zone, and Capitella, in mid emerged and low submerged microhabitats (Table 5). Mean densities of other groups are given in Table 4. "Other" in mid submerged is Callianassa.

Tube-dwelling amphipods were the most consistently numerous type of invertebrate in Area C, a plot of intermediate substrate texture adjacent to the ISP. Bivalves in mid saturated and submerged microhabitats were also relatively abundant (Table 6). Occurring next most abundantly were annelids in saturated and submerged areas. Interestingly, insects

consisting of larval and pupal Diptera, a group generally found almost exclusively in the high tide zone of other areas, occurred in emerged areas of both the mid and low tide zones of Area C. This may have been related to a tendency of flies to lay eggs on the sparse new growth of filamentous algae that covered almost all of the mid tide and low tide emerged microhabitat of Area C. Among tube-dwelling amphipods fused Corophium were the most numerous in all microhabitats. C. stimpsoni occurred primarily in submerged microhabitats, and Grandidierella and Ampelisca were generally scarce (Table 7). Except for two Transennella in low submerged microhabitat, all bivalves were Gemma (Table 6). Lumbrineris was the most numerous annelid in all microhabitats but the high emerged, where few worms were found. Polydorids in low saturated and submerged microhabitat, and Scoloplos in mid saturated and submerged, and Capitella and Mediomastus, in high saturated, also occurred commonly (Table 7). Other organisms included a Cerithidea in high emerged microhabitat, a Hemigrapsus in mid submerged, a Pinnixain in low emerged, four and Callianassa (two in mid submerged and one each in low edge and low submerged).

In the muddy sand flats of Area D, tube-dwelling amphipods were abundant in high submerged and mid and low saturated and submerged microhabitats. Annelids were next most abundant, occurring commonly in all but high emerged microhabitat. Insects (Diptera larvae and pupae) occurred commonly in high emerged microhabitat. Bivalve numbers reached highest densities in mid saturated, low emerged, and high submerged microhabitats (Table 8). All tube-dwelling amphipods were fused Corophium. Lumbrineris was the commonest annelid in all microhabitats with polydorids,

Mediomastus, and Notomastus next most abundant (Table 9). Gemma was the only bivalve species found in the high submerged microhabitat. Transennella was the most abundant bivalve in mid and low tide zones (Table 9). "Other" species include Pinnixa in high and mid saturated and high and low submerged microhabitats and Hemigrapsus in the high saturated microhabitat.

Low densities of total organisms from the sand flats of Area E contrasted with the markedly higher ones from the other areas sampled. With the exception of the high emerged microhabitat of all areas, the high saturated microhabitat of Area B, and the low emerged microhabitat of Area C, the densities of total organisms in Area E were significantly lower than those from the corresponding microhabitats of all other areas (Tables 2, 4, 6, 8 and 10). Tube-dwelling amphipods, all fused Corophium, and sand-dwelling amphipods, all Eohaustorius, reached highest densities in the high emerged microhabitat of Area E. Annelids were the most wide-spread group of organisms and occurred most numerous in saturated and submerged microhabitats and in the low tide zone (Table 10). Few individuals of relatively many annelid species were found in varying frequencies in Area E; some of the species were found in none of the other sampling areas (Table 11). We found the holothurian, Leptosynapta, only in the low submerged microhabitat of Area E during June (Table 10). The two "Other" organisms included in the table were both the gastropod Olivella biplicata.

Our core samples from areas A, D, and E in December and from the invertebrate sampling plot between November and February also differed in

compositions of invertebrate infaunal groups and species (Table 1). Bivalves decreased in relative abundance from the finest to coarsest substrates. Tube-dwelling amphipods were relatively most numerous in the ISP and Area D and occurred at only low densities in areas A and E. Alga-dwelling amphipods occurred at low densities in all areas but Area E. In December the relative abundance of annelids was uniformly high in all areas but that of nemerteans and tube-dwelling amphipods varied unexplainably. Nematostella was found primarily in Area A, Leptochelia only in the ISP and in Area D, and sand-dwelling amphipods, (Eohaustorius), and Leptosynapta only in Area E. Insects were relatively abundant in areas A and D but were absent from Area E. A more detailed description of the infauna of each area in December follows.

Annelids and bivalves were the most abundant organisms in Area A during winter (Table 12). Annelids reached peak abundance in high saturated and submerged microhabitats where polydorids were the most common species found, and the mid submerged microhabitat, where polydorids and Capitella were about equally abundant and the most commonly occurring worms in our cores (Table 13). Capitella and polydorids were also the most abundant annelids in the low tide zone. Bivalves, all Gemma, were most abundant in low submerged and emerged and mid submerged microhabitats. Nematostella and insects were the next most abundant organisms, the former occurring at highest densities in the mid and low tide zones, and the latter in the high tide zone (Table 12). Alga-dwelling and tube-dwelling amphipods, groups that each comprised several species (Table 13), and nemerteans occurred in most of the microhabitats but never at very high densities (Table 12).

"Other" organisms in Area A include Hemigrapsus in high emerged and leptostracans in low submerged microhabitat.

Annelids, tube-dwelling amphipods, and Leptochelia were the most numerous species groups in December from Area D cores (Table 14). Lumbrineris was the most common annelid in all microhabitats with the exception of low emerged, where polydorids were most common (Table 15). Other commonly occurring polychaetes were Mediomastus in high saturated Armandia in mid and low submerged microhabitats, and polydorids in low saturated and submerged microhabitats (Table 15). All tube-dwelling amphipods found were fused Corophium, except for 2 Grandidierella of 99 tube-dwellers in low saturated and 5 of 30 in low submerged microhabitat. Bivalves and nemerteans occurred in most of the microhabitats but never in relatively high densities (Table 14). All bivalves in the mid and low tide zones and 2 of 13 bivalves in high submerged were Transennella; the remainder, in high saturated and submerged, were Gemma. Insects were clearly the most abundant organisms in high emerged microhabitat. "Other" organisms included two caprellids in high emerged, and one Callianassa and two phoronid worms in low submerged.

Annelids and sand-dwelling amphipods were the most abundant species groups found in the Area E December cores (Table 16). All sand-dwelling amphipods were Eohaustorius, except for one Paraphoxus in mid emerged microhabitat. Few individuals of at least 11 species of annelids occurred in all microhabitats sampled. All of the unidentified polychaetes (annelids) in the high tide zone and in mid submerged microhabitat were one species. The most abundant polychaetes identified were Ophelia and

Notomastus in the low tide zone and Mediomastus in mid submerged microhabitat (Table 17).

Systematically collected cores taken from the invertebrate sampling plot between July 1973 and May 1974 also provide information on inter-area variability in invertebrate abundance on the lagoon. Because the sampling methods used in Area C and the ISP were not the same, and because we divided the tide zone of the ISP simply into the high and low halves, the means calculated for Area C and the ISP are not strictly comparable. Nonetheless, if we present the results of the ISP core samples taken from July through October the same way the June Area C cores were presented, they demonstrate the same phenomena shown by the Area C cores: tube-dwelling amphipods were the most abundant organisms in the most microhabitats, with bivalves and annelids as the next most commonly occurring organisms (Tables 6 and 18).

Since Area C was not sampled in December, the winter ISP cores can be presented by microhabitat, to approximate Area C. When this was done (Table 19), annelids were always the most numerous organism group in the microhabitats, followed by tube-dwelling amphipods and bivalves. The peak abundance of Leptochelia occurred in low submerged microhabitat and of insects, in high emerged. Nemerteans occurred in every microhabitat at low densities (Table 19).

Our only information for spring is from the ISP, where annelids were among the most abundant organisms in all microhabitats. Tube-dwelling amphipods were next most often the most abundant organisms in the microhabitats. Tanaidaceans, represented by Leptochelia, was one of the most abundant organism groups in low submerged microhabitat (Table 20).

Microhabitat Distribution of the Infauna

We found that the vertical distribution of organisms in the tidal zone is influenced by their very local distribution in microhabitats as reflected by the fact that the densities of many organisms differed significantly between emerged, saturated, and submerged locations at the same tidal level. In most cases that a significant difference occurred, submerged areas supported higher densities of organisms than emerged or saturated areas, or saturated areas supported higher densities than emerged areas (Table 21). The tendency for total invertebrate densities to be higher in submerged than emerged areas was more prominent in the high and mid tide zone than the low tide zone (Table 21). The percentage of two way comparisons that produced significant differences increased from 5% in the low tide zone to 45% in the mid and high tide zones for annelids, from 20% to 52% for tube-dwelling amphipods, and from 17% to 47% for bivalves ($P < 0.05$, test for the equality of two percentages), but only from 0% to 5% for the nemertean species group, which displayed little sign of microhabitat segregation (Table 21). This suggests that for many organisms, microhabitat distribution, like tidal distribution, is a response to desiccating conditions present on emergent surfaces at low tide.

The only group of organisms that consistently occurred at higher densities in emerged than submerged or saturated microhabitats was insects. A few other exceptions to the rule of higher densities in submerged microhabitat occurred in some areas (Table 21): In Area A the annelid Capitella was significantly most abundant in saturated microhabitats and

significantly least abundant in submerged ones and in areas A and B the bivalve Gemma was significantly most abundant in emerged microhabitats. In the mid tide zone of Area D and low tide zone of Area C Transennella was significantly more abundant in saturated than emerged or submerged microhabitats. Tube-dwelling amphipods were significantly more abundant in emerged than submerged portions of the low tide zone of Area E, probably because the low submerged areas there contained a poorly mixed sediment of sand, gravel, and cobble, a substrate unsuitable for the tube-building habits of these amphipods.

Temporal Variability in Tidal Flat Conditions and the Abundance of Organisms

On the whole, evidence presented below suggests that the foraging conditions at Bolinas during the winter period are less favorable for shorebirds than at other times of the year. The tidal flat is less available during the day and the estuarine algal beds are considerably less extensive during winter than at other times of the year. There is a decline in the abundance of many substrate- and alga-dwelling organisms during winter which is not offset by the increased winter abundance of a few other species groups. During winter there are more water birds competing with the shorebirds for the depleted food resources on the estuary than at other times of the year. Even the important predators of shorebirds are more abundant on the estuary during the winter than at other times of the year.

One notable phenomenon at Bolinas Lagoon (and at other California estuaries) is that the tidal flats are exposed for fewer daylight hours during the winter than at other times of the year. In fact, the predicted number of hours that the tidal flats below 1.4 m are exposed in November and December is almost half that in May and June (Fig. 2A). This is due both to the short daylength and the fact that the highest tides of the month occur mid-day in winter. Further, strong onshore winds, rain, and fresh water run off from the surrounding hills can increase the height of the water in Bolinas Lagoon so that when rain and high tides coincide, the tidal flats can be submerged for most of the daylight hours. Since most rain in the Bolinas area occurs between October and March (Fig. 2A), the actual number of hours of tidal flat exposure in winter is often even fewer than predicted by tide water heights.

Another predictable phenomenon is the seasonal appearance of extensive algal beds on the tidal flats. In the high tide zone of areas with muddy to very fine sand sediments, Vaucheria forms a felt-like mat over the substrate. Beds of filamentous algae, including Enteromorpha, Rhizoclonium, and other species, grow on vast areas of the tidal flat, usually mixing with the top few centimeters of sediment, and remain in place for several months. Broad-bladed Ulva lies awash on the tidal flats and forms beds, particularly in the low tide zones. Gracilariopsis, attached to cobbles in the low tide zone, grows in sandy areas near the mouth of the lagoon during the summer. Algal cycles in the lagoon are well characterized by the amounts of algae covering the ISP for three years (Fig. 3). During the winter and early spring months algal coverage is

minimal, consisting of decomposing Ulva and bits of Gracilariopsis in the low tide zone. Algal coverage first becomes conspicuous by May, when Vaucheria mats begin to form. It reaches maximum coverage in August, then rapidly dies back to a few sparse patches until the following spring. Filamentous alga beds occur from May to October but are most extensive in July and August. Ulva occurs from June to December but forms its most extensive beds from August to November. Bits of Gracilariopsis appear in the ISP August and persist in small amounts throughout winter.

The abundance of amphipods of three genera is closely linked to the algal cycles on the lagoon. The alga-dwelling amphipods, Allorchestes angusta, Ampithoe spp., and Anisogammarus spp., were uncommon on non-alga-covered tidal flats of the lagoon but much more numerous in some algal beds on the flats, especially in low submerged microhabitat (Table 22). In the high and mid tide zones the abundance of alga-dwelling amphipods in the algal beds was usually greater than on nearby barren areas, but variability was too great for the differences to be significant. In the low tide zone the difference was usually significant (Table 22). The close relationship between the extent of the algal beds and the number of alga-dwelling amphipods is also clear in a comparison between the two in the ISP (Figs. 3 and 4): a "bloom" of alga-dwelling amphipods from July through September corresponded to the last 3 months of a 5 month period in which the algal beds were most extensive.

Other groups of organisms also underwent seasonal cycles of abundance in our ISP (Figs. 5, 6, and 7). Tube-dwelling amphipods were most abundant from July through September and least abundant from November through

January (Fig. 5). They were relatively most abundant from April through October (Table 23). Bivalves were most abundant from July through November and least abundant from March through May (Fig. 5). They were relatively most abundant in October and November (Table 23). Annelids were most abundant from November through March and least abundant in June (Fig. 6). They were relatively most abundant from November through May (Table 23). Tanaidaceans, all Leptochelia, were most abundant from January through May and least abundant from July through September (Fig. 6); however, they were never relatively abundant (Table 23). Peaks of insect (larval and pupal Diptera) abundance occurred in November and May (Fig. 7), but insects were always relatively scarce (Table 23). Nemerteans showed no seasonal cycles of abundance (Fig. 7) nor were they ever relatively abundant (Table 23). The highest abundance of total organisms in the ISP occurred from July to September, undoubtedly due to the peaks for amphipods and bivalves (Fig. 5).

Other groups of birds, competitors and predators of the shorebirds, are more numerous in winter than in fall or spring. Surface-feeding ducks, American Coots (Fulica americana), and Mew Gulls (Larus canus) all feed on substrate-dwelling organisms from the tidal flats of the lagoon. These birds are all most abundant on the lagoon during winter. Most duck species do not begin to approach peak numbers until October, and coots and Mew Gulls not until November (Page, unpub. data). Hawks and owls of several species hunt shorebirds on the lagoon daily during winter but are seen there only occasionally during other times of the year (Page and

Whitacre 1975; Page, unpub. data). The presence of these other species undoubtedly puts added pressure on the shorebirds, who are exploiting diminished food resources in winter.

RESULTS

PART II.

SHOREBIRD DIETS

BLACK-BELLIED PLOVER

During all seasons and in all areas from which we collected Black-bellied Plover feces errant polychaetes were the principal prey in over half of each sample examined (Fig. 8). Other prey found in primary quantities in at least some of the samples from each season were sedentary polychaetes, small crustaceans, tube- and alga-dwelling amphipods, immature dipterans, and bivalves. Sedentary polychaetes occurred in 29% to 55% of the samples, but never in more than 30% as a primary prey. Small crustaceans occurred in at least half of each sample, but only from Area D were they major prey in over half of the droppings examined. Tube-dwelling amphipods were important prey during the fall but not the winter period. Alga-dwelling amphipods occurred in a few of the droppings of each sample (Fig. 8) but only as primary prey only during the fall period. Immature dipterans did not constitute more than 29% of any sample and were major prey in only one dropping from each sample. Bivalves occurred in a substantial proportion of each sample but usually only as a trace item. Prey that occurred as primary components in only one sample include oligochaetes and adult insects from Kent Island in winter, and tanadaiceans (Leptochelia) and decapods from Area D in fall. It is apparent that, while errant polychaetes were always prominent elements of the birds' diets, other prey types could occur in a substantial proportion of the samples, in

the fall (Fig. 8). Observations of feeding plovers support this conjecture: the proportion of the Black-bellied Plovers' prey that we could positively identify as annelid increased from 18.7% of 1632 prey items in fall to 54.8% of 1009 prey items in winter (unpubl. data).

The number of polychaete species (or families) that occur in primary quantities in at least one sample increased from 4 in fall to 11 in winter (Fig. 9). During both seasons Lumbrineris occurred most frequently of the polychaetes as a primary prey in the samples. Also found in primary amounts were Platynereis, Scoloplos, and Axiiothella in fall and these species plus Exogone, Eteone, unidentified Nereidae, Orbiniidae, Capitellidae, Glycinde, Nephtys, Polydora socialis, and Boccardia proboscidea in winter.

Amphipods and small crustaceans were the next most prominent prey groups in the Black-bellied Plover's diet (Fig. 8). Small crustaceans comprised ostracods, in 80%, and copepods, in 50% of the total fall sample and ostracods, in 83%, copepods, in 72%, and cumaceans, in 3% of the total winter sample. Because of their small sizes relative to other plover prey, small crustaceans must be taken in large numbers before having a significant food value for the birds, and they were not. While ostracods occurred in greater than trace amounts in about one third of the droppings, they never made up more than a trace of the volume of the individual fecal specimens. Copepods and cumaceans were even less prominent in the diet. Tube-dwelling amphipods, however, did often constitute the bulk of the fecal samples in which they occurred as a primary prey. Corophium with fused urosomes was by far the most commonly occurring tube-dwelling

amphipod in the samples. Grandidierella occurred as a trace item in two of the fall fecal specimens and Corophium stimpsoni as a trace in one of the winter specimens. Allorchestes was the only alga-dwelling amphipod to occur in greater than trace amounts in the feces. It occurred in 33% of the total fall and 3% of the total winter sample droppings. Ampithoe occurred in 23% of the total fall and 3% of the total winter sample droppings. Anisogammarus occurred in 13% of the total fall and 7% of the total winter sample droppings. From the fall sample we examined two dropping that were mostly fragments of Ulva, four more that contained Ulva in primary amounts, and an additional four with Ulva in trace amounts. On several occasions we saw Black-bellied Plovers eating substantial amounts of this alga. Eleven of the 23 plovers we observed feeding in fall and 2 of the 31 plovers in winter made some of their prey capture attempts in algae. We have also seen Black-bellied Plovers pick up and shake Ulva with their bills, and then eat small prey that had fallen from it (unpubl. data).

Decapods identified in the feces included Hemigrapsus oregonensis (the only species found as a primary prey in droppings), which occurred in 7% of the total fall sample, Pinnixa, which was found in 13% of the total fall and 7% of the total winter sample, and Upogebia, which was found in 10% of the total winter sample. We did not positively identify any decapods in the prey we saw Black-bellied Plovers eat in fall but 3 of 1009 prey taken in winter were identified as crabs (unpubl. data). We doubt that when plovers take small decapods we would be able to identify them as such during observations of feeding birds.

Adult insects occurred as primary prey only in the winter Kent Island sample, in which adult Coleoptera constituted a major portion of one dropping. Coleoptera was the only adult insect group we identified in the winter fecal samples. In the fall samples we identified adult Diptera, Coleoptera (Carabidae), and Hymenoptera. However, during both seasons most adult insect remains were too scarce or finely divided to identify, even to order. When adult insects are abundant some individual plovers may specialize on them. During one fall feeding observation of 18 minutes we saw one plover catch 231 flying Diptera adults (plus 71 small unidentified prey taken on the ground).

We identified larval Diptera of the families Anthomyiidae and Dolichopodidae in the fecal samples. During fall only the dolichopodid was found in greater than trace amounts, occurring in primary quantities in one dropping from each of the areas. In winter we found a larval anthomyiid in primary amounts in one dropping and an unidentified larval Diptera in another. Trace remains of an unidentified Diptera pupa were also found in one winter dropping.

Because of the resistant nature of mollusc shells, it is not surprising that they were often found in trace amounts in fecal samples. At least six species of bivalve were identified from the fall and winter samples. Only from the fall samples were we able to identify bivalves that occurred in greater than trace amounts: Gemma from one Pine Gulch dropping, Cryptomya from a Kent Island dropping, and Transennella from an Area D dropping. Bivalves found in trace quantities include the gem clams, Gemma and Transennella, and Protothaca in both seasons, Mytilus in fall, and Macoma

and Mytilidae in winter. The only gastropod identified from the feces was Lacuna, a trace of which was found in the fall Area D sample.

Other prey types were found only in trace amounts. The few Foraminifera taken were so small that it is unlikely that they contributed much to the nutritional needs of the birds. Many of these, and possibly the small crustaceans, may have been ingested incidentally with other prey. Sand and salt marsh amphipods found in the samples included Orchestia traskiana from Kent Island and an unidentified Talitridae from Area D in fall, and an unidentified isopod from Kent Island and Eohaustoriuss from Area D in winter. Fish bones were found in trace amounts in the feces of Black-bellied Plovers feeding on Kent Island and in Area D, fall and winter. We saw plovers capture fish during feeding observations only on Kent Island in winter. Of the 13 birds watched, three were seen eating fish; one plover caught one fish during a 10 min observation, one caught two in a 10 min observation, and one caught three in a 7 min observation (unpubl. data). The only fish that we found on the tidal flat in our substrate sampling, the small arrow gobi, Clevelandia ios, which inhabits the burrows of ghost and mud shrimp, was probably the fish that the plovers caught. Nemerteans may occasionally be taken; we once observed a Black-bellied Plover capture and eat a Paranemertes peregrina in Area D (unpubl. data).

Seeds and terrestrial plant material, taken only in the winter, were probably obtained either when the bird moved up to nearby pastures at high tide or were taken in the estuary after being washed in by winter rains.

Several studies on both the east and west coasts of North America

provide additional dietary information on the Black-bellied Plover. Interestingly, the studies done on the east coast produced results most similar to ours. The stomach contents of one fall migrant Black-bellied Plover collected at the head of Bay of Fundy was dominated by polychaetes, particularly Nereis diversicolor (Hicklin and Smith 1979). The nemertean Cerebratulus lacteus was the next most prominent prey; the gastropods Turbonilla elegantula and Lunatia heros the amphipod Corophium volutator, and dipterans, were each present in very small amounts. From another specimen collected in the same area during May, Hicklin and Smith (1979) found Diptera larvae (Tabanidae and Stratiomyidae) making up 95% of the sample volume with Coleoptera and the gastropods Hydrobia totteni and Dermacentor sp. constituting trace amounts. Baker (1974) observed Black-bellied Plovers foraging during spring and fall migratory stopovers on a Connecticut mudflat. The plovers fed mainly on polychaete worms, with Nereis succinea predominating. Small clams, probably Mya sp., were also taken, although in smaller amounts.

The remaining studies found polychaetes to be of secondary importance in the Black-bellied Plover diet, in comparison to other prey species. Holmberg (1975), in his sample of 9 specimens from a mudflat on Humboldt Bay, California, found that bivalves constituted the major prey items, with Lyonsia californica predominating and Transennella tantilla and Mytilus edulus present in much fewer numbers. Prey items of secondary importance in Holmberg's study include unidentified polychaetes, unidentified nereids, and the gastropod Phillipysia talori. Trace amounts of insects, unidentified crustacea, the amphipod Anisogammarus pugettensis, and

unidentified vegetable matter were also taken. Recher (1966) found that the gastropod Ilyanassa obsoleta made up 67%, the polychaete Neanthes succinea 16%, Gemma gemma 13%, and other bivalves 4% of the prey in stomachs from three birds collected in South San Francisco Bay. McCollough (1981) observed foraging Black-bellied Plovers at staging areas in eastern Maine, during their southward migration and reports that crustaceans, which included Chiridotea coeca and the amphipod Gammarus oceanicus, comprised 27% of the food items taken, polychaetes 18% and gastropods 10%.

SEMIPALMATED PLOVER

Our information on the Semipalmated Plover's diet is restricted to the fall season, although the species is common on Bolinas Lagoon during the fall and spring migration periods (Page et al. 1979). During fall censuses of different feeding areas, over 75% of the Semipalmated Plovers counted were feeding around the muddy basin at the north end of the lagoon, in areas A and B (ibid.). In all areas used they usually fed on dry or damp high tide flats, regardless of the water level. Errant polychaetes, immature dipterans, and oligochaetes were the dominant prey in the fecal sample (Fig. 10). Sedentary polychaetes, small crustaceans, tube-dwelling amphipods, and adult insects occurred as primary items in some droppings, but alga-dwelling amphipods and bivalves only occurred in trace amounts (Fig. 10).

An unidentified oligochaete, Lumbrineris, and the dolichopodid larva were the most prominent prey species in the fecal sample. Lumbrineris was

the most commonly occurring polychaete found in the sample, present in primary amounts in 33% and in trace amounts in 7% of the droppings. Platynereis was a primary constituent of 20% and unidentified Nereidae of 7% of the sample; unidentified Nereidae also occurred in trace amounts in 13% the droppings. Capitella and unidentified Capitellidae were each present in 7% of the feces, with Capitella in primary and Capitellidae in trace amounts. Dolichopodidae larvae were present in primary quantities in 40% and in trace quantities in 20% of the droppings. Other immature dipterans that occurred in primary amounts were the larvae of two species of Ephydriidae which each occurred as primary prey in 13% of the sample; one occurred in an additional 13% and the other in 46% of the droppings in trace amounts. The pupae of the most commonly occurring ephydrid larva was present in 13% of the droppings. Larvae of a species of Anthomyiidae occurred in 27% of the droppings in trace amounts.

Small crustaceans, amphipods, adult insects, and bivalves each occurred in at least 40% of the sample's droppings but seldom in greater than trace amounts (Fig. 10). Ostracods were present in primary amounts in 13% and in trace amounts in 20% of the sample. Copepods were present in trace amounts in 33% of the sample. Corophium with fused urosomes were the only species of tube-dwelling amphipod found in the feces. Trace amounts of Allorchestes was found in 7%, Ampithoe in 7%, and an unidentified amphipod in 13% of the droppings. Adult Diptera and adult Heterocerus each occurred in primary amounts in 7% and in trace amounts in another 40% of the droppings. Immature Heterocerus, not included in Figure 10, occurred in primary amounts in 20% and in trace amounts in 7% of the sample. The only

bivalves found were Gemma, in 7%, and an unidentified gem clam, in 40% of the sample.

Three other studies, each using small samples of Semipalmated Plover stomach contents, suggest diets with some similarities to that at Bolinas. Stomachs from three plovers collected at mudflats in South San Francisco Bay contained primarily Neanthes succinea, and traces of the bivalve Gemma gemma, the gastropod Ilyanassa obsoleta, and unidentified ostracods (Recher 1966). At a staging area in the Bay of Fundy, Hicklin and Smith (1979) collected seven Semipalmated Plovers from intertidal mudflats in fall. The amphipod Corophium volutator made up an average of about one half and adult insects (Diptera and Odonata) about one fourth of the prey found in these stomachs. Jaws of the polychaetes Nereis sp. and Glycera sp. were found in four stomachs and six intact specimens of Heteromastus filiformis were recovered from the digestive tract of one bird. Remains of the bivalve Macoma balthica, and the gastropods Hydrobia totteni and Turbonilla elegantula each made up a small proportion of the stomach contents. McCollough collected a total of six Semipalmated Plovers at four sites and made feeding observations on an unreported number of individuals taking 2,5774 prey items at seven sites on the Maine coast in fall. Results from the observations conflicted with those from the stomachs examined. Larval and adult Diptera were the most numerous prey in four of the stomachs (from two sites), with gastropods, amphipods or isopods, and annelids occurring less commonly. In another stomach he found three gastropods and an annelid and in the sixth stomach polychaetes (primarily Nereis virens), gastropods, amphipods or isopods, and bivalves (primarily Mytilus sp.). In contrast,

he found polychaetes, amphipods and isopods, and oligochaetes, in that order, taken most often by the feeding birds he observed. Collectively, these four studies demonstrate the importance of annelids or dipterans in the fall diet and two studies also indicate that amphipods may be important in some locations.

WILLET

Willetts are the generalists of Bolinas Lagoon's shorebird community, foraging in many areas and microhabitats on the estuary and eating a variety of large and small prey items, particularly various species of crustaceans. Our results on this species, as well as the Long-billed Curlew, are published in a paper that is attached to this report as Appendix 1.

LONG-BILLED CURLEW

The Long-billed Curlew is the only shorebird on Bolinas Lagoon to specialize on large species of prey (Callinassa, Upogebia, and Hemigrapsus). See Appendix 1 for further detail on this species' diet.

MARBLED GODWIT

In fall and winter errant polychaetes were the most prominent prey in the fecal samples of Marbled Godwits feeding on Kent Island and in Area D (Fig. 11). Our fecal samples were obtained from some of the most important godwit feeding areas on the lagoon as reflected by the fact that over 90% of the Marbled Godwits counted in five tidal flat areas around Bolinas Lagoon were feeding in areas C (Kent Island) and D (Page et al. 1979). Sedentary polychaetes and small crustaceans were the prey types of next highest occurrence in the samples (Fig. 11). Decapods were the only other prey to occur in primary quantities in both fall and winter samples. In fall samples, amphipods and fish occurred in greater than trace amounts. Other prey, found only in trace amounts, included Foraminifera, oligochaetes, tanaidaceans (Leptochelia), insects, and molluscs.

The dominance of polychaetes in the godwit's diet was largely due to the occurrence of Lumbrineris, which was the most commonly occurring species in both seasons and areas (Fig. 12). Only from the Kent Island samples did another species, Platynereis bicanaliculata, approach the frequency of occurrence of Lumbrineris. Scoloplos and Axiiothella also occurred in greater than trace amounts in all samples. Unidentified Nereidae and Nephtys occurred slightly more frequently and prominently in fall than winter, while Glycinde and polydorids were slightly more prominent in winter than in fall (Fig. 12). Exogone, Pseudopolydora, and unidentified Capitellidae occurred infrequently and only in some samples. Our observations of feeding godwits confirm the importance of worms in the

diet (unpubl. data). In both fall and winter 71% of the prey taken during feeding observations could be identified as annelids (n=267 in fall and 349 in winter). Since some of the godwits' prey were consumed while the birds' heads were still in the water, other unidentified prey could have also been worms.

Because the small crustaceans (ostracods, copepods, and cumaceans) are minute relative to other small abundant prey, such as tanaidaceans and amphipods, yet are taken more frequently, we suspect they may have been picked up by godwits incidentally. Ostracods were the only small crustacean taken in primary quantities in fall, and were found more frequently than the other two types (in 70% of the total fall sample, compared with 27% for copepods and 17% for cumaceans). In the 28 winter samples ostracods were found nine times and copepods two times in primary quantities; ostracods occurred in 50%, copepods in 46%, and cumaceans in 4% of the winter sample.

Decapods identified in the fecal samples included Pinnixa during both seasons and Upogebia during fall. Only Pinnixa was found in greater than trace amounts. Only 1% of the fall prey and none of the winter prey that we observed godwits eat were classified as large unidentified, the category into which larger decapods such as Upogebia would fall (unpubl. data). Since some prey were consumed with the birds' heads underwater, large unidentified prey could have been taken which we did not detect. However, evidence from the fecal samples suggests that decapods other than Pinnixa (which is a tiny crab that would not be categorized as large, unidentified prey if it were seen eaten) are not major items in the diet.

Amphipods were more prominent in the diet during fall than winter (Fig. 11). Traces of tube-dwelling amphipods (almost entirely Corophium with fused urosomes) were found in a fairly high proportion of the fall sample but only in 20% of the Area D sample were they present in greater than trace amounts. A trace of Grandidierella was found in one dropping from Kent Island. In winter Corophium (fused) was the only tube-dwelling amphipod in the feces. Alga-dwelling amphipods were found only in fall samples. Allorchestes was found in the samples from both areas but Ampithoe and Anisogammarus were only found in the Kent Island sample. Allorchestes was the only alga-dwelling amphipod found in primary amounts. Unidentified Talitridae (either Orchestia or Orchestoidea), primary prey in 10% of the Kent Island sample in fall, were the only crustaceans from the salt marsh / sand beach amphipod or isopod category found (not shown in Fig 11).

Other prey types occurred uncommonly. Although we did not see godwits catching and eating fish, we found fish bones in a few fecal samples, particularly in fall (Fig. 11). Insects constituted a very minor part of the godwits' diet. An adult Coleoptera in fall and a Dolichopodidae larva in winter were the only insects identified in the feces. Most bivalve remains in the feces could not be identified to species although we found traces of a Transennella in the fall and winter samples and Gemma in the fall sample. Gastropod remains could not be identified to species.

North American studies providing additional information on the Marbled Godwit show similarities to our findings in illustrating the prominence of polychaetes in the diet. Recher (1966) found the polychaete

Neanthes succinea making up 76% of the prey, the gastropod Ilyanassa obsoleta 11%, and the pelecypods Gemma gemma, Mya arenaria, and Macoma inconspicua combined 13% in nine godwit stomachs collected from a San Francisco Bay mudflat. Reeder (1951) examined six godwit stomachs from a mudflat in coastal Orange County, California. The polychaetes Scoloplos and Cirriformia were the dominant food items, with nereid and other polychaetes present in lesser numbers in five stomachs. A total of 324 larvae of the shorefly Ephydra were found in another stomach. One to ten shells of the gastropod Melampus were found in five stomachs, and the gastropod, Olivella, and pelecypods Donax and Pecten were minor constituents of one stomach. Holmberg (1975) examined eight stomachs from godwits collected on a mudflat in Humboldt Bay, California. Polychaetes, including Eunereis longipes, made up half and the gastropod Phyllaplysia taylori about a third of the prey found. Unidentified nereids, Leptochelia dubia, Anisogammarus pugettensis, unidentified animal matter, Zostera marina (a marine phanerogram), the alga Enteromorpha, unidentified plant matter, and seeds were all minor constituents of the stomach contents.

All studies demonstrate the importance of polychaetes in the godwit's diet. However, our study differs from the other three, which indicate that gastropods are important food items. While gastropods are not abundant where most godwits feed on the lagoon, crustaceans are. This may explain the godwit's exploitation of crustaceans and the omission of gastropods as primary prey in our study.

BLACK TURNSTONE

The Black Turnstone is common on Bolinas Lagoon from mid July to early May (Page et al. 1979). In fall most turnstones counted in five areas on the lagoon were in Area C on Kent Island; in winter they were distributed fairly evenly over all the areas in which they were counted (ibid.). The distribution of the turnstones on the lagoon reflects their seasonal change in feeding habits. In fall they pick small prey from beneath algae, which they roll back like carpets with their bills. In winter, when the algae have largely died away, the turnstone feed along the rip-rapped and gravelly eastern edge of the lagoon and in the high tide zone at the muddy ends of the estuary where the mud dries into leathery plates; small stones of the rip-rap and leathery plates of mud provide hiding places for small invertebrates, which the birds find when they flip over the rocks and mud with their bills.

Fall and winter are the two seasons for which we have fecal samples. During both seasons alga-dwelling amphipods were the most commonly occurring prey types found (Fig. 10). Tube-dwelling amphipods, small crustaceans, and errant polychaetes also occurred in primary amounts in the fall sample. During winter oligochaetes, errant polychaetes, and immature dipterans each occurred twice as primary prey; decapods and gastropods occurred in about half of the sample but mostly as trace components of the feces (Fig. 10).

The remains in the fall sample comprised mostly a few species of amphipods, small crustaceans, and polychaetes. Allorchestes was the most

common fall prey, occurring in 95% of the sample as a primary prey and 5% as a trace. Corophium with fused urosomes were the next most common prey, occurring in 36% of the sample as a primary prey and 32% as a trace. Other amphipods only occurred in trace amounts: Ampithoe in 27%, Anisogammarus in 14%, and Grandidierella in 5% of the sample. Platynereis was a primary prey in 23% and Lumbrineris a primary prey in 5% of the sample. Ostracods were primary prey in 27% and trace prey in 18% of the sample; copepods were trace prey in 14% of the sample. All other prey types occurred in trace amounts in the feces (Fig. 10). One dropping with adult insects contained an adult dipteran and the immature dipteran found was an Ephydriidae pupa. One dropping contained an unidentified limpet (Acmaeidae), possible obtained by the turnstone on the outer rocky coastline.

The winter sample held a greater variety of prey types than the fall sample (Fig. 10). Again, Allorchestes was the most common, occurring in 78% of the sample as a primary prey and in 22% as a trace. All other amphipods occurred only in trace amounts, Ampithoe in 44%, Anisogammarus and fused Corophium each in 22%, and Corophium spinicorne and an unidentified non-corophid amphipod each in 11% of the sample. Unidentified Nereidae and Platynereis each were primary prey in 11% of the sample, Lumbrineris was a primary prey in 11% and a trace in 11%, and unidentified Capitellidae was a trace in 11% of the sample. Traces of Hemigrapsus oregonensis were found in 11% of the sample and unidentified decapod was a primary prey in 11% and a trace in 22% of the sample. Immature dipterans found as primary prey were an Ephydriidae larva in 11% and a Dolichopodidae larva in 22% of the sample. Traces of the Ephydriidae larva were found in

11% and traces of an Anthomyiidae larva in 22% of the sample. The flies lay their eggs in the leathery mud plates during the summer and fall and the turnstones probably find the resulting larvae when they turn the plates over in winter. Molluscs all occurred in trace amounts: unidentified molluscs, an unidentified bivalve, and an unidentified gem clam each in 11%, unidentified gastropods in 44%, and Lacuna in 22% of the sample.

Connors (1977) provides additional information on the diets of seven Black Turnstones from rocky intertidal habitat near Bodega Bay. Eleven taxonomic groups were represented in the stomachs examined. Mobile crustaceans were the primary prey, including several species of decapod crabs, isopods, and amphipods, all of which were found in five of the seven specimens. One stomach contained primarily polychaetes and another primarily limpets. Other prey found in smaller amounts included mussels, snails, barnacles, pycnogonids, insects, and fish eggs. Connors' results and our study on Bolinas Lagoon show the importance of crustaceans in the Black Turnstone's diet. Discrepancies in the particular crustacean taxa taken in the two studies undoubtedly are due to the different habitats in which the birds were feeding.

RED KNOT

Red Knots are uncommon on Bolinas Lagoon, but most abundant during fall and spring migration (Page et al. 1979). On Bolinas Lagoon they can be found on the flats around Kent Island and in Area D. One of the droppings was collected from Kent Island and eight from Area D. Bivalves

were primary prey in all of the fecal specimens (Fig. 10). Errant polychaetes occurred in 78% of the sample but only in 11% in primary amounts. Gastropods were found in 44% of the sample but only in 11% in primary amounts. Alga-dwelling amphipods and tube-dwelling amphipods each occurred in 11% of the sample in primary amounts; alga-dwelling amphipods also occurred in 11% in trace amounts. Other prey, only occurred in trace amounts and included small crustaceans, Foraminifera, tanaidaceans, and sedentary polychaetes (Fig. 10).

Several species of bivalve were found in the sample. Transennella occurred as primary prey in 56% and in trace amounts in 22% of the sample. Protothaca occurred as a primary prey in 44% of the sample. Gemma constituted primary prey in 22% and trace prey in 22% of the sample. Macoma were primary prey in 11% and trace in 44% of the sample. Traces of Mytilus occurred in 22% and traces of Clinocardium, unidentified gem clam, and unidentified bivalve each occurred in 11% of the sample.

At least five polychaete species were found in the sample. Lumbrineris occurred in primary amounts in 11% and as a trace in 11% of the sample. Glycinde was a primary prey in 11% of the sample. Other species were found only in trace amounts: Exogone in 56%, Nereidae in 11%, Platynereis in 11%, and unidentified Capitellidae in 22% of the sample.

Other prey types occurred infrequently in the sample. Lacuna was primary prey in 11% and a trace in 11% of the sample. Traces of unidentified gastropod were found in 22% of the sample. Corophium and Allorchestes were each primary prey in 11%, and Ampithoe a trace prey in 11% of the sample. The unidentified crustaceans in the sample were

amphipods. Ostracods formed a trace in 22% and copepods a trace in 33% of the sample.

Sperry (1940) and Recher (1966) provide additional information on the diet of the knot in North America. As in our study, both determined molluscs to be the chief prey item of this species. Sperry (1940) collected 219 specimens from the Atlantic and Gulf coast states. He found that molluscs were the chief prey item, constituting 59% of the food volume in his samples. Gastropods were taken more commonly and in greater varieties than bivalves; many of the snails were from fresh water habitat. Of the bivalves, Donax sp. was the principle food item in many of the stomach samples examined; Gemma gemma and Mytilus sp. were less commonly found. Crustaceans constituted 6.9%, insects, 14.8%, king crab eggs, 2%, and unidentified plant food 15.9% of the food volume. Recher (1966) found that the bivalve Gemma gemma made up 55.3% and the polychaete Neanthes succinea 44% of the total food items taken from a mudflat in San Francisco Bay. Contrary to our results, Recher (1966) found gastropods to be of minor importance in the diet of the knot; Ilyanassa obsoleta constituted only 0.7% of the total food taken.

European studies corroborate the evidence that molluscs are important in the diet of the knot (Davidson 1971, Prater 1972, Goss-Custard et al. 1977, Evans 1979, and Evans et al. 1979). Macoma sp. predominated over Hydrobia sp. in all but Evans' (1979) study, where Hydrobia was taken as the chief food; he also found that the polychaete Nereis diversicolor constituted a regular food item. Others found either no indication of polychaetes in the diet (Davidson 1977) or determined that they were minor

prey. Similar to our results, Prater (1972) and Evans (1979) found that crustaceans (particularly Corophium) were taken as secondary prey.

SANDERLING DIET

Sanderlings occur on Bolinas Lagoon from mid-July through late May and are at peak numbers from August through October; during their stay they are always most commonly found in the sandier portion of the estuary, in areas D and E (Page et al. 1979). Fall and spring Sanderling food samples comprised a combination of fecal droppings, regurgitated pellets, and one stomach from a raptor-killed Sanderling in fall, but the winter sample was derived entirely from fecal droppings. During the fall, amphipods and small crustaceans were the most commonly found prey in the sample (Fig. 10). The winter samples was dominated by finely-digested, unidentified crustaceans. In the spring sample, polychaetes, sand- and salt-marsh-dwelling amphipods, adult insects, bivalves, and unidentified crustaceans were the most prominent organisms.

Tube- and alga-dwelling amphipods were the most commonly occurring primary prey in the fall diet (Fig. 10). Species found in primary quantities were Corophium with fused urosomes in 52% and Allorchestes in 57% of the sample. Traces of fused Corophium were found in an additional 19% of the sample. Other amphipods in the fall sample, but occurring only in trace amounts, included Amphithoe in 10%, Anisogammarus in 14%, and Grandidierella in 10% of the sample. Sand-dwelling amphipods found in fall included Eohaustorius, present in 19% as a primary prey and an additional 5% as a trace prey, and Paraphoxus, occurring as a trace in 5% of the sample. The only small crustacean occurring in primary amounts was

Ostracoda. Ostracods were found in a total of 71%, copepods in 10%, and cumaceans in 5% of the fall sample. The tanaidacean, Leptochelia, was the only other species to occur as a primary prey in the fall. The polychaetes Exogone, Platynereis, and Lumbrineris, each occurred as a trace prey item in 10% of the sample, Transennella and unidentified gem clams each in 29%, and the gastropods Alvinia and Lirularia each in 5%.

Although most of the winter fecal specimens were so well-digested that we were unable to identify most of the prey species found in them, we determined that they comprised primarily crustacean fragments. We suspect that at least some of the crustaceans were sand-dwelling amphipods or isopods as these invertebrates lack dactyls or other distinctive parts that are as digestion-resistant as those of some of the other amphipods, tanaidaceans, or decapods found on the lagoon. Primary quantities of sand-dwelling amphipods identified in the sample were entirely Eohaustorius. One dropping contained traces of an isopod. Small crustaceans, tube-dwelling amphipods, and alga-dwelling amphipods occurred much less frequently in the winter than in the fall and bivalves, while still mostly a trace element in the droppings, occurred slightly more frequently in the winter than the fall sample (Fig. 10). In winter, ostracods and Corophium with fused urosomes each occurred as trace items in 9% of the sample and alga-dwelling amphipods were not found at all. Bivalves found in the winter included primary quantities of an unidentified gem clam and traces of Macoma and Transennella and an unidentified gem clam, each in 9% of the sample. Traces of unidentified bivalve remains occurred in 36% of the sample. Other prey types, such as Foraminifera,

polychaetes, tanaidaceans, decapods, insects, and gastropods were found infrequently in the sample as they had been during fall. Species of errant polychaetes found in winter were the same as those found during the fall. In winter, sedentary polychaetes found included Axiiothella in 9% of the sample and unidentified Capitellidae in 18%. Species of decapods and adult insects were not identified. The dropping with the trace of an immature dipteran contained an Ephydriidae pupa and the one with a trace of gastropod, a Lacuna.

In the spring sample, polychaetes, sand-dwelling amphipods, adult insects, bivalves, and unidentified crustaceans were the most frequently occurring primary prey of the Sanderling (Fig. 10). Fish eggs also occurred in primary amounts in one pellet and in trace amounts in another. Polychaetes found in primary amounts included Platynereis and Lumbrineris each in 7% of the sample and Nephtys and Axiiothella each in 13% of the sample. In addition, we found traces of Exogone and Lumbrineris in 7% and traces of unidentified Capitellidae in 13% of the sample. Sand-dwelling amphipods found were Eohaustorius in 7% and Paraphoxus in 27% of the sample. Primary amounts of adult insects were all Staphylinidae beetles; they also occurred in trace amounts in 7% of the sample. Unidentified adult insects occurred in 13% of the sample. Bivalves in primary amounts in the spring sample were Macoma in 13%, Gemma in 7%, and unidentified gem clam in 7%. Traces of Transennella occurred in 7% of the sample. The unidentified crustaceans in three samples appeared to be talitrid amphipods but we could not be certain of their specific identification. Other prey were found only in trace amounts (Fig. 10). Foraminifera occurred in 40%,

ostracods in 7%, and copepods in 7% of the sample. Upogebia and an unidentified decapod each occurred in 7% of the droppings.

Several North American studies provide additional information on the Sanderling's diet. The only other food samples collected from birds feeding on protected tidal flats were taken over an entire year by Couch (1966) at Cultus Bay, Washington. The 25 stomachs from birds feeding on a sandy substrate and 15 from a silt-sand substrate showed little inter-area variability in prey composition. In both substrates, crustaceans, predominantly amphipods, were the major prey taken. Anisogammarus confervicolus constituted over half of the total prey, with Orchestoidea pugettensis and Allorchestes angusta occurring next most commonly. Isopods, decapods, bivalves, insects, Corophium spp., and Paraphoxus sp. each constituted less than 6% of the total prey items. These results parallel our findings on Bolinas Lagoon, particularly in our fall sample of fecal droppings and regurgitated pellets, in which amphipods were clearly the primary prey in the Sanderling's diet. Although our winter and spring samples were similar to the Cultus Bay samples, bivalves and polychaetes seem to be more important prey in our samples than in those from Cultus Bay.

Other reports of prey taken by Sanderlings in North America are of birds feeding on open coast sandy beach, the habitat in which Sanderlings are most commonly found. On Copalis Beach, Washington, in his sample of 33 stomachs, Royal (1939) found that Sanderlings fed primarily on razor clams (Siliqua patula) during the summer and early fall months, when clams of the incoming year class ranged from 5 to 12 mm in length. Other prey included

cockles, terrestrial insects, gastropod egg cases, and fish. In a sample of 25 specimens collected from beaches along the Washington coast, Couch (1966) found results strikingly different from her Cultus Bay sample. On the beach, half the prey items in the sample were razor clams. Crustaceans were clearly of secondary importance, with Eohaustorius washingtonianus making up 6.6%, unidentified crustaceans 5%, and Anisogammarus confervicolus and Allorchestes angusta each 1.6% of the prey items found. Insects and unidentified polychaetes also each made up 1.6% of the prey items. At Salmon Creek Beach, California, Myers et al. (1979), found that Sanderlings foraged primarily on the isopod Exciorolima linguifrons and to a lesser extent on the sand crab Emerita analoga. Reeder (1951), at Point Mugu, Ventura County, California, collected 2 specimens in which immature Emerita made up the entire food mass.

The remaining North American studies considering the Sanderling's diet suggest that this species sometimes may be an opportunistic forager. Pearse (1968) observed Sanderlings scavenging on decaying bivalves and fish on a New Jersey beach. Gochfield and Burger (1980), on a Texas beach, and Rapp and Rapp (1945), on a New Jersey beach, observed Sanderlings scavenging opportunistically on fish carcasses.

In Europe, Sanderlings feeding on beaches were found eating primarily polychaetes and small crustaceans. Evans (1979) found that the nereid worm, Nerine cirratulus and the amphipod Bathyporeia spp. were the most prominent Sanderling prey on beaches in Teesmouth, England. Boere and Smit (1981) report that polychaetes, especially Scolecopsis squamata were the most important prey in the Sanderling's diet, but that crustaceans and

small molluscs were also taken in small numbers on beaches along the Wadden Sea.

WESTERN SANDPIPER

Tube-dwelling amphipods were the most consistently important prey of the Western Sandpiper at Bolinas Lagoon and in the Limantour Estero sample (Fig. 13) and Corophium was clearly the most important tube-dweller eaten (Fig. 14). Corophium with fused urosomes was the only Corophium found in the Bolinas Lagoon diet, except for the spring Area C sample, in which fused Corophium was a primary prey in all and C. stimpsoni a trace item in 20% of the stomach-pumped samples. Three species of Corophium were found in the Limantour sample. Due to spatial and seasonal variability in the diet, other amphipod species, insects, polychaetes, oligochaetes, and bivalves were also each major prey in at least one of the sample sets from Bolinas Lagoon.

Over 90% of the Western Sandpipers counted in the five tidal flat areas on Bolinas lagoon during the fall used the sandy flats of areas C and D for feeding (Page et al. 1979). The most important prey taken from these areas were clearly Corophium and Allorchestes (Fig. 14). In Area C the larvae and pupae of an ephydrid fly also were primary prey in 6 of the 19 samples and trace items in another 6; Gemma was primary in one stomach. All other prey species were found only in trace amounts and in fewer than 30% of the stomachs (Fig. 14). In Area D the only non-amphipod prey that occurred in greater than a trace amount was Lumbrineris in one stomach. Polydora

socialis was the polydorid species found in the Area D sample set. The same ephyrid larvae and pupae found in the Area C sample occurred in a third of the Area D sample but only in trace amounts. As in Area C, other prey species occurred rarely and in trace amounts (Fig. 14). Four stomachs pumped at a daytime high tide roost (Area J in Fig. 1) contained primarily insect prey, which were probably obtained on the high tidal flats at the edge of the salt marsh or in the marshy vegetation of the roost area; one stomach also contained major amounts of Corophium. Traces of Streblospio, alga-dwelling amphipods, Grandiderella, and Gemma were probably the remains of prey taken earlier on low tide feeding grounds (Fig. 14). A sample of Western Sandpiper stomachs from nearby Limantour Estero in fall contained prey very similar to those found at Bolinas. Corophium spp. were prominent in the diet, fused Corophium being a major item in 35%, C. stimpsoni in 25%, and C. spinicorne in 50% of the stomachs. Other species of polychaetes, alga-dwelling amphipods, insects, and gem clams were of minor importance compared to Corophium (Fig. 14). Polydora nuchalis and P. socialis were found in 10% and 15% of the Limantour samples, respectively.

The tidal flat distribution of the small number of Western Sandpipers that usually winter on Bolinas Lagoon is very similar to that for fall (Page et al. 1979). In our small sample of winter stomachs (one from Area A, two from Area D, and three from dusk in Area H) Corophium is a primary prey in four and Capitella, an ephyrid larva, and Transennella each in one stomach. These species, other polychaetes, and Allorchestes also occurred as trace items in additional stomachs (Fig. 14).

During the spring censuses of the tidal flat areas, almost 85% of the

Western Sandpipers counted were feeding in areas C and D; during this period on some days over 30,000 migrant westerns can be found on the lagoon (Page et al. 1979). In areas C and D Corophium was the most important prey in the diet as in the fall but Allorchestes, also important during the fall was found in trace amounts in only one of the spring stomachs (Fig. 14). Prey types found in markedly more stomachs in the spring than other seasons include Foraminifera, Polydora nuchalis, Pseudopolydora, Streblospio, Capitella, and seeds in Area A, Lumbrineris and Polydora socialis in Areas C and D, Transennella in Area D, and Exogone and Gemma in all three areas (Figs. 13 and 14). Leptochelia, prominent in the winter sample, was also important in the spring area C and D samples (Fig. 13).

Several studies report diet information for the Western Sandpiper. Couch (1966) and Holmberg (1975) each report amphipods or tanaidaceans dominating the stomach contents. In the stomachs and feces of birds from Mugu Lagoon and Upper Newport Bay Quammen (1980) found sedentary polychaetes, oligochaetes, and unidentified crustaceans most commonly of all invertebrate prey types. Studies and observations made in south San Francisco Bay report ostracods (Recher 1966) and the brine fly Ephydra millbrae (Murie and Bruce 1935) as major prey of Western Sandpipers feeding at different locations there. On a southern California beach Reeder (1951) found immature sand crabs Emerita constituting 75% of the food volume in seven stomachs, with insects making up the balance of the prey contents.

Couch (1966) found that tube- and alga-dwelling amphipods were the major prey taken in four different substrate types on False and Cultus Bays, in

Washington. Corophium constituted from 12% to 58% of the total food items taken and predominated over the alga-dwelling amphipod, Anisogammarus confervicolus, in all but one of the samples taken from a mud-sand substrate on False Bay where A. confervicolus comprised 60% and Corophium 12% of the sample. At Bolinas Lagoon A. confervicolus didn't occur in any Western Sandpiper diet samples but at Limantour was a primary prey in 5%. Couch (1966) reports that Anisogammarus is usually found swimming actively in shallow water at the edge of the beach or in pools of water left by the receding tide. Couch (1966) also found that the alga-dwelling amphipods, Allorchestes angusta and Ampithoe spp. were taken, although they constituted less than 0.5% of the samples. In one of Couch's (1966) sample sets, which is markedly smaller than her others (consisting of 5 stomachs, while others range from 17 to 19), insects are the major prey taken, making up 74% of the sample. The isopod Rocinela was taken in trace amounts in all but one of the sample sets, in which it constituted 18% of the stomach contents. Unidentified pelecypods, gastropods, polychaetes, cumaceans, and seeds were considered minor prey items.

Holmberg (1975) examined 20 stomachs of birds collected from a mudflat in Humboldt Bay and found that the tanaidacean Leptochelia dubia made up 57% of the prey in the stomachs, the amphipod Anisogammarus pugettensis 27%, the bivalve Transennella tantilla 5%, unidentified nereids 2%, and diptera larvae 6.8%. In 21 specimens from a pasture near the bay, he determined that insects were taken almost exclusively, constituting 98.8% of the stomach contents; unidentified vegetable matter made up the

remaining 1%.

Quammen (1980) examined 14 stomachs and 42 fecal samples of Western Sandpipers from a muddy sand substrate on Mugu Lagoon and 12 stomach and 64 fecal samples from the muddy upper reaches of Newport Bay. At least half of one or both sample types from both areas contained oligochaetes, polydorids, Streblospio, Capitella, and unidentified crustaceans. Other prey, occurring less regularly or commonly in the samples were Nereis, unidentified polychaetes, ostracods, Corophium, the gastropods Cerithidea, Acetocina, and Tryonia, the bivalve Cryptomya, and seeds.

Recher (1966) found that ostracods made up 63% of the stomach contents in 78 specimens taken from a mudflat in south San Francisco Bay. Other prey, of lesser importance, included the gastropod Ilyanassa obsoleta, Gemma gemma, Nereis succinea, and unidentified amphipods. Murie and Bruce (1935) observed 2000 to 3000 Western Sandpipers feeding opportunistically with four other species of birds on conspicuous brine fly (Ephydra millbrae) swarms near the edge of south San Francisco Bay. The sandpipers were chasing down and eating adult brine flies on a paved road.

The studies presented here show strong variability in the Western Sandpiper's diet. Couch's (1966) and Holmberg's (1975) results indicate the importance of amphipods and tanaidaceans, while Quammen (1980) demonstrates that of polychaetes, oligochaetes, and molluscs. Our findings substantiated the importance of all five of these taxonomic groups in the species' diet.

LEAST SANDPIPER

While the Least Sandpiper's diet varied seasonally and among different areas on Bolinas Lagoon, amphipods and insects were consistently important prey (Fig. 15). Amphipod genera taken included tube-dwellers Corophium and Grandidierella, alga-dwellers Allorchestes, Ampithoe, and Anisogammarus, and a talitrid, probably Orchestia. Immature dipterans, including larvae of a species of Anthomyiidae and Dolichopodidae and larvae and pupae of a species of Ceratopogonidae and two species of Ephydriidae, were generally more prominent in the diet than other insects. Other insects identified in the samples were adult dipterans, the coleopterans Heterocerus sp. (adults and immatures) and Staphylinidae (adult), Hymenoptera (including Braconidae) adults, and a Hemiptera (Saldulidae). Small crustaceans, polychaetes, oligochaetes and bivalves occurred inconsistently in the diet and were more prominent in winter and spring than in fall. Small crustaceans included ostracods, copepods, cumaceans, and the tanaidaceans Leptochelia and Tanais. Polychaetes included a nereid, Exogone, Boccardia proboscidea, Polydora nuchalis, and Capitella. The only bivalves found in the samples were Gemma and Transennella. Of minor importance in the diet were Foraminifera, gastropods, and seeds. Foraminifera occurred as a minor prey in 17 to 21% of the Area A samples, 21% of the Area B samples, and 3% of the Area C sample, suggesting that they were somewhat restricted as prey to birds feeding on the finer substrates of the lagoon. Gastropods occurred occasionally in stomach contents but the only species that was ever identified was a Littorina sp. from Area D in winter. Occasionally seeds were found in stomach contents but never in great enough abundance to

be more than a minor constituent.

In fall, the species' period of peak abundance on the lagoon, about half the Least Sandpipers counted in five tidal flat areas occurred in Area C and the rest were fairly evenly divided between areas A, B, and D (Page et al. 1979). Amphipods were important prey in all these areas and particularly in areas C and D. Among the tube-dwellers, Corophium always occurred more commonly than Grandidierella and was clearly the most important prey taken from Area D (Fig. 16). Alga-dwelling amphipods occurred in at least half and as a primary prey item in at least one stomach from each area (Fig. 15). Allorchestes was the most important alga-dweller in areas B and C and the only one from Area D. In Area A where alga-dwellers were less important than in other areas Ampithoe occurred about as often as Allorchestes and was a major item in one stomach. Most striking is the relative absence of insect prey in samples from Area D and to a lesser extent from Area C than the area A and B samples (Fig. 16). This trend is most pronounced among the dipteran larvae and pupae but also holds for adult insects. Adult and immature insects were also a prominent part of the diet of Least Sandpipers coming to a daytime high tide roost in Area J (Fig. 15). Polychaetes taken in fall include a nereid from Area B, Exogone and Capitella from Area D, and Boccardia proboscidea from Area J (Fig. 15).

In winter, about two thirds of the Least Sandpipers counted fed in the fine sediments of areas A and B and the rest were found in Area D (Page et al. 1979). In winter stomach samples prey that predominated during the fall period, i.e. insects in Area A and Corophium in Area D, diminished

slightly in importance and more prey types were taken than during fall. For example, in the Area A winter sample oligochaetes, sedentary polychaetes, and bivalves, all relatively absent from the fall sample, became prominent as trace items and each occurred in at least one stomach as a major prey (Fig. 15). The species of sedentary polychaetes taken by Least Sandpipers in winter were Boccardia proboscidea in 6.3%, Polydora nuchalis in 62.5% (and as major prey in 12.5%) and Capitella in 12.5% of the stomachs. In addition to changes in the prey types taken from fall to winter, there are differences in the species of prey between the two seasons, particularly in Area A (Fig. 16). There the relative fall abundances of Corophium and Grandidierella are reversed and neither genera occurred in greater than trace amounts in any stomach in winter. Among the alga-dwelling amphipods in Area A, Allorchestes and Ampithoe, which occurred in the fall sample, were absent and replaced by Anisogammarus in the winter sample. Ephydriidae larvae and pupae, the most important dipteran prey in fall, are the least prominent in winter when Ceratopogonidae larvae and pupae, and Dolichopodidae and Anthomyiidae larvae occur most prominently as primary prey. Adult Diptera and Hymenoptera occurred in the fall but not the winter or spring samples. Ostracods, copepods and cumaceans, collectively shown as small crustaceans in Fig. 15, only occurred as major prey, or as trace items, in more than 41% of the stomachs, from the Area H sample in winter (Fig. 15). Copepods and ostracods were a major prey in 43% of this sample. Tanaidaceans were important dietary components in the winter samples from areas D and H where Leptochelia was the only tanaid found; in the Area A spring sample Tanais

sp. occurred in trace amounts and Leptochelia was absent.

In spring 80% of the Least Sandpipers occurring on the tidal flat censuses were found in Area A (Page et al. 1979); our only spring diet sample (six stomachs) came from Area A. Major differences in the diet between the spring and other times of the year are the appearance of errant polychaetes, the greater importance of alga-dwelling amphipods, and the diminished occurrence of immature diptera during spring (Fig. 15). As in winter, the only genus of alga-dwelling amphipod found was Anisogammarus (Fig. 16). In the spring sample C. spinicorne was found in 50% and fused Corophium in 17% of the stomachs; in all samples from other seasons and areas only fused Corophium were identified. Errant polychaetes (Nereidae), often as primary prey, and Tanais, only in trace amounts, were also more commonly found in spring than at other times of the year in Area A.

Six other studies reporting diet information for Least Sandpipers in estuarine habitat showed various results but found primarily small tube- and alga-dwelling amphipods, tanaidaceans, ostracods, isopods and insect prey. Couch's (1966) results were the most similar to ours. In a small sample of five stomachs collected from birds feeding in sandy and silty substrates in Cultus Bay, Washington, she found primarily Corophium sp., chironomid larvae, and Cyclorhapha sp. larvae. From three birds feeding in mud-sand substrate at False Bay, Washington, Corophium sp. and Anisogammarus confervicolus were the only important prey. Hicklin and Smith (1979), working at tidal flats in Nova Scotia, and Holmberg (1975) working at Humboldt Bay, California demonstrate the importance of amphipods and other small crustaceans in estuarine locations. Stomachs contents of

eight of nine birds collected by Hinklin and Smith were almost entirely Corophium volutator and the ninth was mostly the isopod Chiridotea caeca with lesser amounts of the cumacean Oxyurostylis smithi. Prominent prey reported in Holmberg's (1975) study were Anisogammarus pugettensis and Leptochelia from 11 birds feeding on the tidal flats and unidentified insect prey from 18 birds feeding in nearby pastures. Interestingly, the three studies done in South San Francisco Bay produced the results most different from ours. In 38 stomach's collected near Palo Alto, Recher (1966) found primarily ostracods and, to a lesser extent, molluscs, the polychaete Nereis succinea, and unidentified amphipods. In contrast to Recher's study, Anderson (1970) and an undated report by the California Department of Fish and Game (hereafter CFG) found primarily insect remains in the stomachs. Anderson noted that five birds collected in fall had eaten primarily adult insects: unidentified corixids, dipterans, and coleopterans, while three collected in winter had eaten primarily larvae of the brine fly Ephydra cineria. The CFG report noted that the 20 Least Sandpiper stomachs examined contained primarily unidentified coleopterans and dipterans; corixids and several species of molluscs were much less numerous in the sample.

Studies of the Least Sandpiper diet done in the eastern Canadian arctic and at a freshwater pond in Illinois reported only insect prey. Brooks (1967) found aquatic insects in three early fall-collected Least Sandpipers and non-aquatic insects in one bird collected in October. Baker (1977) found dipteran larvae, primarily Chironomids, from 33 birds collected at Churchill, Manitoba.

DUNLIN

Dunlin occur at Bolinas Lagoon between mid-October and late April; during their stay almost all that were counted in the five tidal flat areas were found in areas C and D. In winter areas C and D were about equally important to feeding birds and in spring about 80% fed in Area C and about 15% in Area D (Page et al. 1979). However, since all of our stomach-pumped Dunlin samples were taken from birds coming in to evening roosts, we do not know specifically where the individuals had been feeding before they were captured. Tube-dwelling amphipods were major prey in over 70% and both errant and sedentary polychaetes in over 20% of the stomachs during both seasons; tanaidaceans, alga-dwelling amphipods, bivalves, and gastropods were also taken occasionally as major prey. Foraminifera, oligochaetes, small crustaceans (ostracods, copepods, cumaceans), decapods, insects, and seeds were only taken in trace amounts.

In winter errant polychaetes, sedentary polychaetes, and tube-dwelling amphipods were about equally prominent and were clearly the most important prey types taken (Fig. 17). Lumbrineris was the polychaete most frequently taken as primary prey, followed by Capitella, Boccardia proboscidea, Polydora nuchalis, and Scoloplos (Fig. 18). Exogone, Eteone, nereids, unidentified polydorids, Polydora socialis, Streblospio, and Axiiothella were taken only in trace amounts. Corophium and Grandiderella were the only amphipods that occurred in more than 10% of the stomachs in greater than trace amounts in winter; Allorchestes, Anisogammarus, Transennella,

and Lacuna were the only other prey that occurred in at least one stomach in greater than trace amounts (Fig. 19).

The spring and winter diets of the Dunlin were similar although there were some changes in the relative abundance of some prey. The winter occurrence as primary prey of both polychaete types was approximately twice that of spring while the spring occurrence of both bivalves and gastropods was over twice that of winter (Fig. 17). Spring changes in the polychaetes taken include a decrease in the occurrence of Lumbrineris and Capitella, the complete disappearance of Scoloplos, Polydora nuchalis, and Boccardia proboscidea, and the appearance of Exogone, Nereidae, and Polydora socialis as major prey items (Fig. 18). Transennella and Lacuna were the molluscs taken in greater than trace amounts (Fig. 19).

Six other studies providing information on the Dunlin's diet on the North American west coast differ in the prey taxa reported taken. Couch (1966) found that amphipods were the most important prey in 34 stomach samples from two bays in Washington. Anisogammarus confervicolus constituted 82% of the prey found in the stomachs of birds feeding in the muddy substrate of False Bay, but only 36% from the sand flats on Cultus Bay where it was about as common in the stomachs as Orchestoidea pugettensis, which constituted 41% of the prey items. Corophium sp., in Cultus Bay, and Paraphoxus sp., in False Bay were taken much less commonly than the above two species and other taxa were only taken in trace amounts. Stomachs from five Dunlins collected by Couch on a sand beach in Washington contained only Hymenoptera of the families Braconidae, Formicidae, and Tenthredinidae.

Recher (1966), working near Palo Alto in San Francisco Bay, and Quammen (1980), working at Mugu Lagoon, Ventura County and at Newport Bay, Orange County, California both found the contents of stomachs they examined to be dominated by annelids. Contents of 46 stomachs from near Palo Alto comprised 70% Neanthes succinea, while unidentified amphipods, ostracods, the gastropod Ilyanassa obsoleta, and the bivalves Gemma gemma, Mya arenaria, and Macoma inconspicua occurred much less commonly (Recher 1966). Sedentary polychaetes, oligochaetes, and unidentified crustaceans, each occurred in all of the six stomach specimens and in over 75% of 56 fecal droppings collected by Quammen (1980) in Mugu Lagoon. Dominant polychaetes were Streblospio and polydorids, with Capitella occurring less commonly. Other prey detected in a macroscopic analysis of the samples included the gastropods Acetocina, Tryonia, Chione, the bivalve Macoma, cumaceans, and seeds. Streblospio, polydorids, Capitella, oligochaetes, and unidentified crustaceans were also the dominant prey found in 28 fecal droppings collected in Newport Bay (Quammen 1980).

Holmberg (1975) looked at stomach contents of 15 Dunlins collected from a mudflat in Humboldt Bay, California, and found that the pelecypod Transennella tantilla made up 26.4%, Leptochelia dubia 25.0%, Anisogammarus pugettensis 7.0%, and Zostera marina seeds 33.4% of the contents. Other prey of minor importance included trace amounts of unidentified polychaetes and insects, the amphipod Caprella sp., and unidentified vegetable matter.

Stomachs from nine birds collected on salt ponds in San Francisco Bay by Anderson (1970) and seven birds collected from South San Francisco Bay

by CFG (und. rep.) contained prominent amounts of bivalves; the birds taken at the salt ponds also had eaten many brine flies Ephydra cineria. Bivalves, Macoma, Gemma, or Mytilis, made up over half the stomach contents from the salt pond birds and Gemma constituted over half the contents of the birds from the Bay with Macoma inconspicua and Mytilis occurring much less commonly. Other prey found in both samples, all in trace amounts, included unidentified polychaetes, amphipods, ostracods, insects, and molluscs.

In some of the recent Palearctic studies of Dunlin diet, the gastropod Hydrobia and the polychaete Nereis are both considered major prey items (Bengtson and Svensson 1968, Burton 1974, Evans et al. 1979, and Goss-Custard et al. 1977). Similarly, Davidson (1971) found that Hydrobia occurred as primary prey in stomach samples, along with unidentified polychaetes, and Fuchs (1975) found Hydrobia in primary amounts in two of nine stomachs he examined. Although Davidson did not mention nereid worms, Fuchs found many Nereis mandibles in two and a few in five of the nine stomachs in his sample. Fuchs felt, however, that the jaws were probably persistent in the stomachs, which over-represented their importance in the diet. It's likely that other polychaetes may be underestimated in the European studies. Goss-Custard et al. (1977), indicate that the polychaete Nephtys was also important in the Dunlin's diet, although it occurred in fewer stomachs than Nereis. They also suspect that more spionid worms were taken than the few found in their samples, especially since these worms were abundant in areas where the Dunlin fed. Worms without prominent jaw parts, as soft-bodied prey, are

very poorly represented in stomach contents. Evans et al. (1979) found that small oligochaetes were present in 65% of the esophageal samples they examined although digestion had rendered them unidentifiable in the birds' stomachs. This led them to suspect that they were probably taken as major prey items in all of their specimens.

Other prey taxa were usually found much less frequently than Hydrobia and Nereis in the diet studies of Dunlin in Europe. Davidson (1971), Evans et al. (1979), and Burton (1974) found that amphipods occurred as secondary prey items, while the results of Goss-Custard et al. (1977) and Bengtson and Svensson (1968) indicated that they were of minor importance in the diet. This result is interesting in light of the relatively great abundance of Corophium volutator at some of the study sites. With the exception of Burton (1974), whose results indicate Talitrus saltator as a secondary prey item and Bengtson and Svensson (1968) who found traces of Gammarus, these studies found Corophium as the only amphipod represented in the diet. Clams were taken infrequently; Macoma was reported as a secondary prey item by Davidson (1971) and Evans et al. (1979), but only as a minor prey item by Goss-Custard et al. (1977). Bengtson and Svensson (1968), Fuchs (1975), and Evans et al. (1979) all found that insects were fairly important in the diet, whereas Goss-Custard et al. (1977) and Burton (1974) consider them minor prey items.

Arctic studies on the diet of Dunlin indicate that insects are taken almost exclusively (Baker 1977, Holmes 1966). Brooks (1967) also found that insects predominated in the overall diet in his two samples from a fresh water pond in Illinois.

DOWITCHERS

Page et al. (1979) described occurrence patterns of dowitchers on Bolinas Lagoon and found the two species to be largely non-overlapping except in spring. Short-billed Dowitchers are common from early July to late October and very uncommon from November through mid March. Long-billed Dowitchers arrive in very small numbers in some years as early as the beginning of August but most birds do not arrive until September and from then on their numbers build to a winter population size of over 100 birds. From mid March through May, while Long-billed Dowitcher numbers are declining, large numbers of migrant Short-billed Dowitchers stop at the lagoon. We rarely find the two species occurring together on the lagoon. Long-billed Dowitchers inhabit the muddier areas at the north and south ends of the lagoon, particularly favoring the gravelly creek mouths on the Pine Gulch Creek delta and along the northeast edge of the estuary. Short-billed Dowitchers are mostly confined to sandier flats from the northeast end of Kent Island (Area C) south to Area D.

SHORT-BILLED DOWITCHER

The importance of prey types that we found in Short-billed Dowitcher food samples from fall and spring birds differed markedly: in fall fecal samples alga-dwelling amphipods were clearly the most important prey type, while in spring stomach-pumped samples tube-dwelling amphipods, sedentary polychaetes, and errant polychaetes were the most prominent prey (Fig. 17).

Given the occurrence patterns described above for dowitchers on Bolinas

Lagoon and the species' habitat selection, it is not surprising that during fall about 80% of the dowitchers in the tidal flat census areas were in Area C; another 15% were in Area A (Page et al. 1979). Ten of the 12 fall fecal samples we collected in fall were from birds feeding in or near Area C, the other two were from Area D. Alga-dwelling amphipods were major prey items in all, errant polychaetes and tube-dwelling amphipods in three, and ostracods in one of the 12 samples. Allorchestes was a primary component of all, and Ampithoe and Anisogammarus were each primary components of one sample (Fig. 19). The six other prey types found only occurred in trace amounts and, with one exception, in only one fecal sample (Fig. 17). Nereidae, Lumbrineris and Scoloplos were the only polychaetes to occur as major prey (Fig. 18). Fused Corophium and Grandidierella were the only tube-dwelling amphipods to constitute more than a trace of a sample (Fig. 19).

The habitat preference and occurrence patterns of the two species is also reflected by dowitcher's distribution on the tidal flat during spring: 55% of those counted in the five tidal flat areas were in Area C and 35% were in Area A (Page et al. 1979). Stomach-pumped samples of Short-billed Dowitchers feeding in Area C were dominated by fused Corophium and C. stimpsoni although Ampelisca was also found twice, including once as a primary prey item (Fig. 19). Short-bills took at least 15 species of polychaetes in spring, including 8 species which occurred at least once as a primary prey, and 7 which occurred only in trace amounts in any stomach (FFig. 18 plus a species of Orbinidae that occurred in one stomach). The only other invertebrate that was found at least once as a major prey was

Gemma (Fig. 19).

Reeder (1951) found that polychaetes constituted major prey items in the diet of five Short-billed Dowitchers collected from a mudflat in coastal Orange County, California. Nereids and cirratulids made up most of the food in four of the five stomachs. Prey of secondary importance included spionid worms and an ephydrid larva each in one stomach, small gastropods and Melampus sp. in three stomachs, and 27 otoliths representing at least seven individual fish of a mud-burrowing goby, probably Clevelandia, in one stomachs.

Several eastern North American studies provide additional information on the diet of Short-billed Dowitchers. Sperry (1940) examined 191 stomachs, 180 of which were from Atlantic coast states and the remainder from Michigan, Ontario, and Saskatchewan. Major prey items included insects, which made up 29% of the food volume in the stomachs, nereids and trace amounts of other unidentified worms which made up 27%, and molluscs which made up 21%. The gastropods Melampus and an unidentified nassarid, and the bivalve Gemma gemma were all represented in the samples. Other prey taken uncommonly included unidentified plant food and horseshoe crab eggs. Hicklin and Smith (1979) and McCollough (1981) demonstrate the importance of both amphipods and polychaetes to dowitchers at staging areas in northeastern America. Corophium volutator was an important prey species for short-bills in both studies and Gammarus oceanicus was commonly taken at one of the study sites visited by McCollough (1981) in Maine. McCollough (1981) also reports that the polychaetes Nereis virens and Clymenella torquata were important prey at one of his sites. Other prey

taken less frequently included oligochaetes, bivalves, and crustaceans. Hicklin and Smith (1979) examined 15 specimens collected from mudflats in Minus Basin, Nova Scotia. The most abundant prey items included Corophium volutator, which made up 70.3% , and the polychaetes Nereis sp. and Glycera sp. which made up 24.9% of the food volume; other prey included several species of gastropods, seeds, an isopod, a bivalve, and insects.

Mallory and Schneider (1979) suspected that Short-billed Dowitchers were taking primarily eggs of the horseshoe crab (Limulus) during August on mudflats of Kingston and Duxbury harbors, Plymouth, Massachusetts. The dowitchers fed in areas where this prey was particularly abundant (and other prey less so) and probed 5 to 6 cm deep, corresponding to the depth of the Limulus eggs. Schneider and Harrington (1981), also working at Kingston and Duxbury harbors, report results that are similar to those of Hicklin and Smith (1979) and McCollough (1981) in that amphipods and polychaetes were found as major prey. Stomachs from two birds feeding on mud substrate contained more than 50% (by volume) identifiable remains of the polychaete Clymenella torquata; those from two birds feeding on sandy substrate contained over 50% (by volume) the amphipods Acanthohaustorius millsii and Trichophoxus epistomus. Less commonly taken prey included Acanthohaustorius and Trichophoxus from the muddy habitat, the amphipod Protohaustorius deichmannae and the gastropods Mitrella lunata and Nassarius trivittatus from the sandy habitat and a nereid polychaete and the clams Tellina agilis and Gemma gemma from both habitat types. They noted that undigested Gemma gemma were found in the intestines of all four stomachs, suggesting this small clam may not be a nutritionally important

part of the diet. Baker (1977) in the eastern Canadian arctic found that plant seeds and insects were both taken as major prey items on the breeding grounds of this species.

The studies of Hicklin and Smith (1979), McCollough (1981), and Schneider and Harrington (1981) together with our studies indicate the importance of both polychaetes and amphipods in the Short-billed Dowitcher's diet. Sperry (1940) indicates that insects are important in this species' diet at fresh-water habitats. In all studies, bivalves were either secondary or minor prey items.

LONG-BILLED DOWITCHER

Winter is the only period for which we collected dietary information for the Long-billed Dowitcher. During winter Area A was the most important dowitcher feeding area of the five we monitored (Page et al. 1979) although birds could often be found feeding in fine sediments with gravel admixtures at the creek mouths along the northeast shore of the lagoon in areas similar to A. Sedentary polychaetes occurred in all but one fecal sample and as a major prey in over 60% of the 19 examined; Capitella was the most commonly taken species, followed by Streblospio, Polydora nuchalis, and Boccardia proboscidea. Pseudopolydora, Boccardia hamata, and Polydora socialis only occurred in trace amounts (Figs. 17 and 18). Tube-dwelling amphipods, particularly Corophium, but also Ampelisca and Grandiderella, was the second most commonly occurring prey type (Figs. 17 and 19).

Errant polychaetes, ostracods and copepods, bivalves, and oligochaetes each occurred fairly commonly in the fecal samples but only rarely as major prey items (Fig. 17). Unidentified nereid, Glycinde, and Tressus were the only species that occurred as major prey of the latter group.

Sperry (1940) examined the stomachs of 99 Long-billed dowitchers, 30% of which were collected in Utah and the remainder from Alaska south to Southern California and east to South Dakota, Colorado, and Texas. His results show that insects were the major prey taken in the overall diet. Dipterans, chiefly in larval forms, made up 58% of the insects taken, while coleopterans made up 11%. Other food taken included unidentified crustaceans, molluscs, polychaetes, and plant material. Sperry's (1940) results show little similarity to ours, but since much of his collecting was done at fresh water sites, this discrepancy is expected.

DOWITCHER SPP.

Several studies providing dietary information on dowitchers do not distinguish between the two species in their results. Recher (1966) studied the diet of 27 dowitchers from a mudflat near Palo Alto and found that Nereis succinea made up 71% of the prey in the samples, Ilyanassa obsoleta 10%, ostracods 10%, Gemma gemma 6%, and other pelecypods 3%. Holmberg (1975) examined 40 unidentified dowitcher specimens collected from a mudflat on Humboldt Bay. The Pelecypod, Transennella tantilla made up 42.3% of the prey in the stomachs, unidentified polychaetes 25.7%, nereids 6.6%, the amphipod Anisogrammarus pugettensis 6.5%, the

gastropod Lyonsia californica 2.3%, and unidentified vegetable matter 14.9%. Minor prey items included trace amounts of pelecypods, isopods, and insects. Quammen (1980) examined 12 stomach and 20 fecal samples of unidentified dowitchers from a mud substrate on Magu Lagoon. Prominent in the samples were sedentary polychaetes; Streblospio occurred in 100% of the stomachs, seeds in 100%, Polydora in 83%, and Capitella in 50%. Oligochaetes were found in 58% and unidentified crustaceans in 33% (with each occurring in over 60% of the fecal samples). Other prey included the polychaetes Ophelia) and a maldanid, the gastropods Acetocina, Tryonia, and Chione, the bivalves Protothaca and Macoma, ostracods, and Corophium. Quammen (1980) also examined 4 stomach and 60 fecal samples of birds from a sand-mud substrate in Newport Bay and found similar results. The polychaetes Streblospio, Polydora, and Capitella were all represented as major prey items in the microscopic analysis of stomach and fecal samples. Oligochaetes were only detected in the fecal pellets, occurring in 83% as were crustaceans in 58%. In a macro-analysis gastropods, bivalves, insect larvae, and seeds were all fairly well represented.

DISCUSSION AND CONCLUSION

Any synthesis of the information on shorebird diet requires an awareness of the biases associated with each of the various methods employed by researchers. Techniques for determining the prey taken, discussed below, include the indirect method of observation of feeding birds and the direct methods of using stomach, esophageal, regurgitated pellet, and fecal samples from the birds.

Observation of feeding birds is a method for which it is often possible to obtain a standardized estimate of prey intake and feeding success rates. While the method works quite well for large shorebirds that eat prey that can be discerned by an observer, we suspect that observers may make many errors in determining whether a small shorebird has captured and swallowed a prey after a capture attempt. The difficulties of quantifying foraging efforts of the smaller species can sometimes be overcome if the observer can closely approach the bird or if foraging efforts are filmed. Feeding observations can be made on a large number of individuals and for a large number of prey captures making it easy to obtain sufficient sample sizes, even when spatial and temporal variability is being measured. Feeding observations also can be used to examine individual variability and differences between individuals, if birds are uniquely marked. The main drawback of the method is the degree of accuracy to which prey can be identified. Unless large, distinctive prey are taken, identification is extremely difficult even to broad categories; this is especially true when the substrate on which the bird is feeding contains many similar-sized and similarly colored prey. Small prey are difficult to identify because of

their size alone. In fact there are few circumstances in which feeding observations alone can provide adequate information on the specific prey shorebirds are eating.

A commonly employed method to more directly determine the kinds of prey being eaten is to collect the bird and examine its stomach contents. Prey in stomachs are found in all stages of digestion so that the distinctiveness of hard undigestible parts, the skill of the observer in identifying dismembered invertebrates and the degree of magnification used to examine the sample all become important variables in the determination of the contents. Organisms with digestion-resistant hard parts such as gastropods and bivalves and to a lesser extent decapods and amphipods are relatively easy to identify and tally in a sample compared to more readily digested organisms such as annelids. If annelids are divided according to whether they have conspicuous digestion-resistant jaw parts, such as in the Nereidae, or lack them, such as in the Spionidae, the importance of magnification becomes apparent. Many nereid jaw parts are actually visible to the naked eye but the only traces left by spionids, digestion-resistant setae, require a magnification of 100 to 1000X before identification is possible. Tallying the number of spionids represented by the setae presents an enormous problem because it means knowing the number of setae per worm and whether or not the entire worm was actually eaten. At a magnification of 100X, only a small part of a food sample can actually be examined for setae without the expense of hundreds of hours of effort. Thus a subsampling method is required for setae and with it the need to insure the subsample is representative of the whole. In the extreme cases

of prey, such as anthozoans, with no digestion-resistant parts the organisms are digested so rapidly after entering the stomach that there is little if any chance of finding them. As a result of all the factors discussed above and the differences in digestion rates between prey, each type taken by shorebirds has its own probability of being detected. The factors on which this probability is based are difficult to quantify although an estimate of a detection bias is essential in order for volumetric or numeric methods of enumerating prey consumption to not produce results with misleading accuracy. These biases are seldom considered by researchers, though most coastal diet studies report invertebrates' food resources comprising a wide array of organism types.

As an alternative or supplement to stomach contents, esophageal contents have been used by a few workers to examine shorebird diets (Rundle 1982). The contents of the esophagus digest very little, if at all, so that prey rendered unrecognizable within minutes of entering the stomach are easily recognized when in the esophagus. The bias associated with digestion is thus eliminated by using esophageal contents and the relative abundance of shorebird prey in an individual's esophagus is an accurate reflection of what has recently been eaten. It should be pointed out, however, that because of the rapid passage of food through the esophagus, the sample will necessarily contain the prey obtained over a very brief foraging period. In fact, 26% of the esophagi examined by Rundle (1982) were empty or contained only traces of food, even though he collected only actively feeding shorebirds. Thus, the number of birds needed to adequately sample the relative frequency of occurrence of invertebrates in

the diet needs to be larger than if stomach contents are used. Since other factors, such as spatial and temporal variability in diet, can also increase the necessary sample size, the exclusive use of esophageal contents may require the sacrifice of an unacceptably large number of birds.

Stomach-pumped samples, regurgitated pellets and fecal samples are methods we and others have used to increase the number of samples that could be obtained and/or to avoid sacrificing birds. All three methods share the limitations of stomach-content analysis, except for the need to sacrifice birds and the concomitant ceiling on sample size. Of the three methods stomach-pumped samples are the most similar to collected stomachs in the information provided on diet. Nevertheless, the pumped sample provides an unknown portion of what is in the stomach and the size of the material pumped out is restricted by the diameter of the tube (straw) on the pump. Consequently stomach-pumped samples could be biased against large prey that had not digested to the point that parts could pass through the straw. The seriousness of this potential bias can be evaluated through feeding observations by revealing the proportion of large and small prey in the diet.

Fecal samples and regurgitated pellets share the limitations and advantages of stomach-pumped samples and also allow for the collection of samples under circumstances where birds cannot be captured for stomach pumping. Weighted against this, however, are additional drawbacks. The material in pellets and fecal samples is more digested than in stomach-pumped samples, in many instances resulting in an even greater bias

in the relative representation of various prey in the sample. For feces, there is the added problem in the time required for different types of organisms to pass out of the alimentary canal and the delay between the time the prey are eaten and when the sample is obtained. The latter can be of particular importance when trying to measure spatial variation in a species' diet if the birds tend to change feeding areas regularly or if samples are collected at communal roosts. An additional problem associated with the use of pellets is that they are readily produced when prey with chitinous exoskeleton or calcareous shells are consumed at a high rate. Consumption of the same prey at a slower rate (allowing more leisurely and complete mechanical and chemical digestion) or of more easily digested prey at a faster rate need not necessarily lead to pellet regurgitation but instead to fecal elimination.

All studies of diet need as their basis some measure of the availability of potential prey; often this measure requires an estimate of spatial and temporal variation. Substrate sampling, most frequently using cores that are sifted for invertebrates, is the most frequently used and probably the best way to measure the availability of the resource. Often this is tedious and time-consuming. Moreover, abundance of prey within a core does not necessarily relate precisely to availability as both the depth of the organism in the substrate and the compaction of the substrate can affect the prey's availability to the shorebird predator.

In trying to determine the most important shorebird prey at Bolinas, we have tried to keep in mind the limitations imposed by our methodology, as outlined above. In comparing our results with other workers' even greater

limitations have been encountered because of the variety of methods used to collect dietary samples, the differing abilities of workers to detect prey in the samples, and the varying levels of detail available on the nature of the food resource in the area where the shorebirds were feeding. Despite these limitations we believe it is possible to draw some generalizations on the importance of various invertebrate groups as prey of shorebirds at Bolinas and elsewhere. In making these generalizations, especially where selection of certain prey types is inferred we have used the following assumption: if shorebirds eat the same amounts (and the same size-class for prey of highly variable size) of a particular prey or prey type, the occurrence rate of that prey in a particular type of dietary sample should be similar 1) within a species, 2) for different species, 3) at different locations, and 4) at different seasons.

We conclude this report by summarizing the importance in shorebird diet of the major invertebrate types on Bolinas Lagoon.

FORAMINIFERA

Foraminifera do not appear to be major shorebird prey at Bolinas or other locations. Foraminiferans were found in more than trace amounts in only the Area A stomach-pumped sample from Western Sandpipers at Bolinas Lagoon. Trace amounts of Foraminifera were found in the dietary samples of many species including fall and winter Black-bellied Plover samples, the fall godwit samples, the Red Knot sample, fall and spring Sanderling samples, fall and winter Western Sandpiper samples, fall, winter and spring

Least Sandpiper samples, winter and spring Dunlin samples, the spring Short-billed Dowitcher sample and the winter Long-billed Dowitcher sample. Our sieves, with 1 mm openings, were too coarse to retain foraminiferans so that we obtained no information on the abundance of these protozoans in the lagoon. However, Hedman (1975) describes numerous species of Foraminifera from Bolinas lagoon and reports several as common to extremely abundant in tidal flat areas used by shorebirds. Consequently it appears that foraminiferans are largely ignored or go undetected by foraging shorebirds at Bolinas. Foraminifera have not been reported to be a significant component of the diet of shorebirds in any other studies either.

ANTHOZOANS:

We found no evidence that anthozoans were eaten by any shorebird but their detection was unlikely as they lack digestion-resistant hard parts. This leaves only undigested specimens as the potentially recognizable evidence of anthozoans in food samples. Workers in other locations were also unable to find anthozoans as shorebird prey either because they are not taken or because they are too difficult to detect in food samples. Since anthozoans are neither abundant or widespread at Bolinas they should be of only minor importance as shorebird prey, were they taken.

NEMERTEANS:

We faced the same difficulties in finding nemerteans in food samples

that we did for anthozoans. Nemerteans are eaten at least occasionally by Black-bellied Plovers as we saw one eat a Paranemertes during a feeding observation (unpubl. data). McCollough (1981) also observed a Black-bellied Plover eating the nemertean Cerebratulus lacteus on the Bay of Fundy, indicating that use of nemerteans is not limited to our study site. At Bolinas nemerteans are not abundant but they are widespread over the tidal flat and therefore could be prey of at least minor importance in the diets of shorebird species that prey regularly on polychaetes. The only methods likely to produce evidence of their consumption by shorebirds would be feeding observations and analysis of esophageal contents.

OLIGOCHAETES:

We had no indication that oligochaetes were the principal prey of any shorebird in any location or season at Bolinas Lagoon; however oligochaetes have occurred abundantly enough in Semipalmated Plover and Western Sandpiper dietary samples to suggest these worms may have been important prey of at least these species in some locations and seasons. Dietary samples of individual Black-bellied Plovers, Black Turnstones and Least Sandpipers also contained more than trace numbers of setae indicating the further importance of oligochaetes in shorebird diets. Trace numbers of oligochaete setae were also found in some Marbled Godwit, Dunlin, Short-billed Dowitcher and Long-billed Dowitcher dietary samples. Our lack of information on the distribution of oligochaetes over the tidal flat prevents us from making any further statement on the importance of these

organisms as prey relative to their occurrence on Bolinas Lagoon. Most other workers do not report oligochaetes as shorebird prey but this is not sufficient evidence of the lack of importance of oligochaetes as shorebird food since the methodology employed by most workers was insufficient to prove the absence of these organisms in the diet. Quammen (1980), who examined shorebird fecal samples under high magnification, found oligochaetes in fecal samples from Western Sandpipers, Dunlins, American Avocets (Recurvirostra americana) and unidentified dowitchers. McCollough (1981) found traces of oligochaetes in Semipalmated Sandpiper (Calidris pusilla) and Semipalmated Plover stomach contents. Evans et al. (1969) found undigested oligochaetes in 65% of the Dunlin esophagi examined from Teesmouth, England and report that they are digested within a few seconds after entering the stomach. Obviously oligochaetes cannot be dismissed as unimportant shorebird prey in dietary studies unless workers examine esophageal contents or make a high magnification search for the tiny setae in stomach or fecal samples.

POLYCHAETES:

Polychaetes are probably second only to amphipods in overall importance as shorebirds' prey on Bolinas Lagoon; in winter they are probably the most important prey type on the lagoon. They were found in the diet samples of all species although they appear to be taken very infrequently by the Long-billed Curlew (Stenzel et al. 1976).

Generally errant polychaetes occurred more commonly than sedentary

polychaetes in the samples for most species. Errant polychaetes occurred in all dietary samples except that of the Least Sandpiper in winter. They were prominent in Black-bellied Plover and Marbled Godwit fall and winter samples and in the Semipalmated Plover sample. They were categorized as a primary prey in a substantial proportion of the spring Sanderling and spring Short-billed Dowitcher samples and they were primary prey in part of the Black Turnstone fall and winter samples, the Red Knot sample, the fall and spring Western and Least Sandpiper samples, the spring Dunlin sample, the fall Short-billed Dowitcher sample and the winter Long-billed Dowitcher sample.

Sedentary polychaetes were more prominent than errant polychaetes in the Western Sandpiper spring sample, the Least Sandpiper Area A winter sample, and the Long-billed Dowitcher winter sample. Sedentary polychaetes also were categorized as a primary prey in a substantial proportion of the Dunlin winter and the godwit fall and winter samples. We found them to be primary prey in part of the Black-bellied Plover fall and winter samples, the Semipalmated Plover sample, the fall Sanderling sample, fall and winter Western Sandpiper samples, all Least Sandpiper samples and the Dunlin spring sample. The only samples lacking sedentary polychaetes were the curlew samples, the winter Black Turnstone sample and the fall Sanderling sample.

The species most frequently taking polychaetes were the plovers and, with the exception of the curlew, the longer billed sandpipers. Of all the shorebirds studied polychaetes were most prominent in the diets of the Black-bellied Plover, the Semipalmated Plover, the Marbled Godwit, the

Dunlin, and the dowitchers.

We suspect that the importance of polychaetes in the diet of most shorebirds has been underestimated because many workers studying food samples fail to use high enough magnifications to detect setae. When polychaetes are found they tend to belong to the Nereidae, a family characterized by large digestion-resistant mandibles that are frequently visible under low magnification. Despite the almost-certain study bias against the discovery of polychaetes in diet samples, they have been reported to be important components of the diet of the Black-bellied Plover, Semipalmated Plover, Marbled Godwit, Dunlin and Short-billed Dowitcher in one or more studies besides ours. The evidence that polychaetes are important shorebird prey is thus broad-based despite the bias against their detection.

SMALL CRUSTACEANS:

Our category called small crustaceans comprises ostracods, cumaceans and copepods, each group made up of species too small to be retained in our screened substrate samples from Bolinas Lagoon. We found small crustaceans in all but the spring Least Sandpiper and fall and winter Long-billed Curlew samples; however, frequently they were only recorded in trace amounts. They were primary prey in a substantial proportion of the fall and winter Black-bellied Plover and Marbled Godwit samples, the fall Black Turnstone samples and the winter Least Sandpiper sample. Semipalmated Plovers, Sanderlings, Western Sandpipers and both dowitcher

species had primary amounts of small crustaceans in part of the sample from at least one season.

Ostracods were detected in fecal and stomach-pumped samples far more frequently than cumaceans or copepods. Ostracods are easily detected in samples by their fairly digestion-resistant shells whereas cumaceans and copepods were usually only found as intact specimens. Potential differences in digestion rate between the different small crustaceans combined with our lack of knowledge of their abundance in shorebird feeding areas limits our ability to determine the relative importance of the three subgroups of small crustaceans to shorebirds. Compared to amphipods, polychaetes, insects and bivalves they probably are of relatively minor importance in the diet. Except for ostracods which Recher (1966) reported as prominent prey in Least and Western Sandpiper stomach contents from a San Francisco Bay study site, small crustaceans have rarely been reported as shorebird prey in dietary studies.

TANAIDACEANS:

Tanadaiceans, of which only Leptochelia dubia was a significant prey, were found in the diet of all species except the Long-billed Curlew, the Semipalmated Plover and the Long-billed Dowitcher. They were prominent prey in the winter Least and Western Sandpiper samples and occurred in more than trace amounts in part of the Black-bellied Plover fall sample, Sanderling fall and winter samples, Western Sandpiper spring sample, and

Dunlin fall and winter samples. Except for curlews, Semipalmated Plovers and Long-billed Dowitchers, they were present in trace amounts in most other samples. Tanaidaceans are widely used and are therefore important prey of shorebirds at Bolinas, particularly in winter when Leptochelia occurs abundantly in parts of the lagoon. It is unlikely that shorebirds foraging on amphipods would ignore Leptochelia as the two prey taxa share behavioral traits. Holmberg (1975) has reported that Leptochelia is eaten by some shorebirds at Humboldt Bay but elsewhere tanaidaceans have not been reported as important shorebird prey.

AMPHIPODS:

Our study suggests that overall amphipods are eaten more than any other prey type on Bolinas Lagoon, particularly in the fall. We found them in the diet of all species and they were the prominent prey in the fall and winter Black Turnstone samples, the fall Sanderling sample, fall, winter and spring Least Sandpiper samples, winter and spring Dunlin samples, and fall and spring Short-billed Dowitcher samples. Although amphipods occurred in primary amounts in a substantial proportion of the fall Black-bellied Plover sample, and at times appeared important in the Willet's diet, they were clearly most important to the small shorebirds. Semipalmated Plovers, Red Knots and Long-billed Dowitchers were the only small shorebirds not found to have amphipods as a primary prey in a substantial proportion of at least one season's dietary sample.

Tube-dwelling amphipods were the most commonly taken amphipod group. We found them to be absent only in the Long-billed Curlew and in the spring Sanderling dietary samples. They were the most important prey of the fall Sanderling sample, the fall, winter, and spring Western Sandpiper samples, the fall and winter Dunlin samples, and the spring Short-billed Dowitcher sample. They also occurred as a primary prey in a substantial proportion of the fall Black-bellied Plover sample, the fall Black Turnstone sample and the winter Least Sandpiper sample. Invariably one or more species of Corophium was the main tube-dweller taken.

Alga-dwelling amphipods were secondary in importance to tube-dwellers in the overall shorebird diet. Unlike use of tube-dwellers, heavy use of alga-dwellers was restricted primarily to the fall period. Alga-dwellers made up the prominent part of the fall dietary samples of the Short-billed Dowitcher, Least Sandpiper, Western Sandpiper, Sanderling and Black Turnstone. They were also important fall Willet prey. The only species preying heavily on alga-dwellers at other seasons were Black Turnstones in winter and Least Sandpipers in spring.

Sand-dwelling amphipods appeared as important prey only in the Sanderlings' diet, undoubtedly because this is the only small shorebird that feeds in large numbers where sand-dwellers are common. Amphipods living in the salt marsh were eaten by Willets and Long-billed Curlews. Most shorebirds do not feed in the salt marsh except during times when the tidal flats are inundated. Therefore salt marsh dwellers are seldom encountered and rarely appear in the diet of most species.

Amphipods size, abundance, and nutritional value are very likely the prime factors promoting their heavy use by shorebirds at Bolinas. Most amphipods are small enough that they can be swallowed by even the smallest shorebirds but they are not so small that too little nutritional value is gained through the capture of each one. They are widespread and abundant on and close to the surface of the tidal flat, causing them to be frequently encountered by foraging birds. Finally, they are easily digested compared to prey such as molluscs.

Globally, amphipods are considered important shorebird prey as they are reported in the diets of many species from numerous coastal locations around the world.

ISPODS:

Isopods were not prominent prey in any of the shorebird diet samples we examined. In fact, we rarely found them in even trace amounts in dietary samples. Most areas where shorebirds fed were devoid of isopods so their absence in the diet was expected. Except for Sanderlings feeding on sand beaches in the Bodega Bay area, shorebirds have not been shown to take many isopods in other areas. We can only conclude from this that isopods are generally less important to shorebirds than most other prey groups. Whether their lack of importance results from the lack of isopod availability to shorebirds or the bird's food preferences is a question we cannot answer from the available data.

DECAPODS:

The large size and deep burrowing habits of decapods limit their accessibility to foraging shorebirds. Except for the small and relatively scarce crab Pinnixa, most decapods at Bolinas grow too large to be swallowed intact by any except the larger shorebird species. Even the larger shorebirds frequently dismember decapods before swallowing them (Stenzel et al. 1976). Certain decapods such as Hemigrapsus and Callianassa are abundant but inaccessible in long burrows at Bolinas Lagoon. They are eaten only by Long-billed Curlews which extract them from the burrows using their long bills or by Willets which steal them from the curlews or find the decapods outside burrows. Thus, decapods are only incidental prey in the diet of all but relatively few shorebirds at Bolinas. Except for Long-billed Curlews and Willets, and a few other species eating Emerita on sandy beaches, decapods are not reported as important shorebird prey from other locations either.

INSECTS:

Insects can be divided into two broad categories by their accessibility to shorebirds. One category, adult insects, was found at least as a trace item in all diet samples except that of the Red Knot. Adult insects never appeared to be the most prominent prey in a sample although they were taken in at least primary amounts in a substantial proportion of the spring Sanderling, fall Western Sandpiper and fall Least Sandpiper samples.

Frequently we were unable to determine whether trace insect remains in samples represented tidal flat species or terrestrial species that had been stranded in the lagoon. However, except for the spring Sanderling sample, which contained insects with which we were unfamiliar samples with primary amounts of adult insect prey usually contained Diptera, Hymenoptera or Coleoptera from the tidal flat community.

We found larval and pupal Diptera in fewer diet samples than adult insects but found that immature dipterans were the prominent prey in the Semipalmated Plover sample and fall and winter Least Sandpiper samples. They were also a primary prey in a substantial proportion of the fall Western Sandpiper sample from one area on the lagoon. Larval and pupal insects generally occurred below the substrate surface and were relatively inactive compared to the adults. Immature dipterans are limited in importance as shorebird prey to species such as the Least Sandpiper and Semipalmated Plover that feed frequently on the higher flats in the muddier areas of Bolinas Lagoon where the immature dipterans are concentrated. Most species of shorebirds, by focusing their foraging efforts on the lower tide level flats encounter the immature dipterans relatively infrequently.

While this and other studies have shown insects to be important prey of only a few of the smaller shorebird species in tidal flat habitat there are three habitats where insects are of prime importance in shorebird diets. These are salt evaporators, bodies of fresh water, and terrestrial habitat. In these areas insects usually are the most abundant potential prey and, consequently, are heavily preyed upon. Therefore we must conclude that insects are one of the shorebirds' most important prey, especially since

they are the most important prey of most species on the breeding grounds.

GASTROPODS:

Except for the predation of Willets on Cerithidea and small salt marsh-dwelling snails, gastropods are seldom eaten by shorebirds on Bolinas Lagoon. Besides the Willet sample they were found in primary amounts only in Red Knot and Dunlin samples. Cerithidea occurs abundantly in submerged microhabitat at the edge of the salt marsh but snails are largely absent from the rest of the tidal flat, giving shorebirds limited opportunity to prey on them. This may explain why they are taken by so few species at Bolinas and many other locations. Other workers seldom report gastropods as major shorebird prey; notable exceptions are only for the Dunlin and Knot in Europe where Hydrobia is a prominent prey of these and at least one other shorebird species not covered in this report and for the knot in some North American locations. Gastropods have distinctive, digestion-resistant shells which are easy to detect in samples, so the lack of reports indicating their use by many shorebirds suggests that gastropods are not as important shorebird prey as polychaetes, amphipods, insects or bivalves.

BIVALVES:

The majority of bivalve species at Bolinas Lagoon rapidly grow too large to be taken by most shorebird species. However, Transennella and

Gemma are two abundant species that are tiny enough to be taken by all shorebirds. Although we found bivalves in most dietary samples, generally they were present only in trace amounts or, if in primary amounts, they did not occur in the majority of the sample. Bivalves were the most prominent prey of the Red Knot, a species differing from others in its extensive use of molluscs. Some Willets also ate large numbers of a variety of bivalves and gem clams were a primary prey in a substantial proportion of the Area A spring Western Sandpiper sample. Bivalves were taken much more abundantly than gastropods by all species at Bolinas but they were also distributed much more abundantly over the tidal flat.

Other workers frequently report bivalves in shorebird diets but usually not as major prey. An exception was Holmberg's (1975) study at Humboldt Bay where bivalves were reported as major Dunlin, dowitcher and Black-bellied Plover prey. Anderson (1970) also reports bivalves as major prey in Dunlin samples from San Francisco Bay salt evaporation ponds. In general, reports of bivalves in shorebird stomachs are numerous enough to indicate they play an important role in shorebird diets. However, given the ease with which bivalves can be detected in dietary samples and that bivalves are generally not the most numerous prey in the samples, the importance of bivalves to shorebirds must be less than that of insects, amphipods and polychaetes.

HOLOTHUROIDEANS:

Holothuroideans of a suitable size for foraging shorebirds were limited

in distribution to tidal flat areas used by relatively few shorebirds. We found no evidence that any shorebird ate holothuroideans on Bolinas lagoon but expected this as we knew of no way to identify digested specimens. We found no reports of holothuroideans in the diet of any shorebird from any other location. These organisms are probably scarce where most shorebirds feed (based on reports of prey availability) and it is to be expected therefore, that even if workers were able to identify digested remains in diet samples that holothuroideans would seldom be found.

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	Area				
	<u>A</u>	<u>B</u>	<u>C</u>	<u>D</u>	<u>E</u>
Anthozoans	2 (2)	1	1 (1)	0 (0)	0 (0)
Nemerteans	2 (2)	1	2 (3)	2 (2)	2 (0)
Annelids	5 (5)	3	3 (5)	5 (5)	5 (5)
Alga-dwelling Amphipods	0 (2)	0	1 (2)	0 (2)	0 (0)
Sand-dwelling Amphipods	0 (0)	0	0 (0)	0 (0)	4 (4)
Tube-dwelling Amphipods	4 (2)	4	4 (3)	4 (4)	4 (1)
Tanaidaceans	0 (0)	1	1 (2)	2 (4)	2 (0)
Insects	2 (4)	2	2 (2)	4 (4)	0 (0)
Bivalves	4 (4)	4	4 (3)	2 (2)	0 (0)
Holothuroideans	0 (0)	0	0 (0)	0 (0)	1 (2)

Table 1. Categories of occurrence for infaunal organisms in barren (non-alga-covered) microhabitats of five areas on Bolinas Lagoon in June and in December (in parentheses) 1973. 0 = did not occur in our barren core sample nor was otherwise found; 1 = occurred rarely in our barren core samples or was found rarely during other exploratory sampling; 2 = occurred in several but not all microhabitats sampled but never abundantly, relative to other organisms in the microhabitat; 3 = occurred in all microhabitats sampled but never relatively abundantly; 4 = occurred in several but not all microhabitats sampled and, in some, relatively abundantly; 5 = occurred in all microhabitats sampled and, in some, relatively abundantly. Substrates of areas grade from fine mud in Area A to sand Area E. Area C winter data is approximated from the invertebrate sampling plot as described in Methods.

	Mean Number / Core							
	(Standard Error)							
	<u>H Em</u>	<u>H Sa</u>	<u>H Su</u>	<u>M Em</u>	<u>M Sa</u>	<u>M Su</u>	<u>L Em</u>	<u>L Su</u>
Anthozoans			0.2 (0.1)	0.2 (0.2)	1.3 (0.5)			0.4 (0.4)
Nemerteans			0.9 (0.9)	0.1 (0.1)			0.3 (0.2)	0.1 (0.1)
Annelids	3.9 (1.5)	6.2 (1/1)	9.7 (1.8)	4.4 (1.3)	20.1 (3.1)	0.3 (0.2)	2.3 (0.8)	2.1 (1.2)
Tube-dwelling Amphipods			1.3 (0.6)	3.6 (1.4)	10.3 (1.6)	12.9 (2.2)	8.6 (4.7)	25.0 (7.1)
Insects	0.3 (0.2)	0.1 (0.1)						
Bivalves		0.2 (0.2)	15.9 (3.1)	152.6 (20.9)	24.2 (6.8)	49.9 (13.8)	35.3 (9.2)	12.0 (3.2)
Other	0.1 (0.1)						0.1 (0.1)	
Total	4.3 (1.5)	6.6 (1.2)	28.0 (4.2)	160.9 (64.4)	56.0 (8.5)	63.1 (14.7)	46.7 (6.4)	39.7 (5.8)

Table 2. Mean number of organisms per core from Area A microhabitats sampled in June 1973. Standard errors in parentheses. Nine cores were collected from each microhabitat: emerged (Em), saturated (Sa), and submerged (Su) substrates of the high (H), mid (M), and low (L) tide zones.

	<u>H Em</u>	<u>H Sa</u>	<u>H Su</u>	<u>M Em</u>	<u>M Sa</u>	<u>M Su</u>	<u>L Em</u>	<u>L Su</u>
Annelids	(35)	(56)	(87)	(40)	(181)	(3)	(21)	(19)
Polydorids	100	98	64	25	4	67	14	16
<u>Streblospio</u>			32		4		48	63
<u>Capitella</u>			3	75	92	33	38	21
<u>Heteromastus</u>		2			1			
Tube-dwelling Amphipods			(12)	(32)	(93)	(116)	(77)	(225)
<u>Corophium</u> spp.			100	78	100	1	16	1
<u>Grandidierella</u>				12		38	23	30
<u>Ampelisca</u>				9		61	61	69

Table 3. Percent composition of annelid and tube-dwelling amphipod species or species groups from the June 1973 sampling of Area A. See Table 2 for abbreviations. Total numbers of annelids and amphipods found in parentheses.

	Mean Number / Core						
	(Standard Error)						
	<u>H Em</u>	<u>H Sa</u>	<u>H Su</u>	<u>M Em</u>	<u>M Su</u>	<u>L Em</u>	<u>L Su</u>
Nemerteans		0.1 (0.1)				0.1 (0.1)	
Annelids	3.3 (0.9)	1.9 (0.8)	1.6 (0.5)	1.5 (0.4)	0.3 (0.2)	2.1 (0.7)	3.0 (1.0)
Tube-dwelling Amphipods			6.2 (1.4)	0.3 (0.2)	8.5 (1.0)	31.3 (2.4)	34.4 (2.8)
Tanaidaceans							0.3 (0.2)
Insects	0.1 (0.1)	0.4 (0.3)					
Bivalves			1.6 (0.7)	149.2 (31.9)	53.8 (13.2)	0.1 (0.1)	0.1 (0.1)
Other					0.2 (0.2)		
Total	3.4 (0.9)	2.4 (0.7)	9.3 (2.0)	151.0 (32.0)	62.8 (12.9)	33.7 (2.3)	37.9 (2.7)

Table 4. Mean number of organisms per core from Area B microhabitats sampled in June 1973. Standard errors in parentheses. Nine cores were collected from each high and low tide microhabitat and six from each mid tide microhabitat: see Table 2 for abbreviations.

	<u>H Em</u>	<u>H Sa</u>	<u>H Su</u>	<u>M Em</u>	<u>M Su</u>	<u>L Em</u>	<u>L Su</u>
Annelids	(30)	(17)	(14)	(9)	(2)	(19)	(27)
<u>Scoloplos</u>						16	26
<u>Polydorids</u>	100	100	100	89		53	22
<u>Streblospio</u>						26	33
<u>Capitella</u>				11			7
<u>Mediomastus</u>					100		
Tube-dwelling Amphipods			(56)	(2)	(51)	(282)	(310)
<u>Corophium</u> (fused)			91		4	5	7
<u>Corophium stimpsoni</u>						28	24
<u>Corophium spinicorne</u>						1	
<u>Grandidierella</u>			4	50	86	4	12
<u>Ampelisca</u>			5	50	10	63	58

Table 5. Percent composition of annelid and tube-dwelling amphipod species or species groups from the June 1973 sampling of Area B: see Table 2 for abbreviations. Total numbers of annelids and amphipods found in parentheses.

	Mean Number / Core									
	(Standard Error)									
	<u>H Em</u>	<u>H Sa</u>	<u>H Su</u>	<u>M Em</u>	<u>M Sa</u>	<u>M Su</u>	<u>L Em</u>	<u>L Sa</u>	<u>L Su</u>	
Nemerteans	0.1 (0.1)	0.6 (0.3)	0.3 (0.2)	0.2 (0.1)	0.3 (0.2)		0.1 (0.1)	0.2 (0.1)	0.4 (0.2)	
Annelids	0.6 (0.2)	2.9 (2.7)	3.6 (0.9)	1.8 (1.1)	9.9 (1.1)	7.7 (0.9)	1.1 (0.4)	4.2 (1.0)	6.9 (1.0)	
Alga-dwelling Amphipods			0.1 (0.1)							
Tube-dwelling Amphipods		5.9 (2.3)	32.6 (3.2)		20.8 (3.8)	27.8 (3.3)	1.8 (0.8)	28.2 (6.9)	45.1 (3.6)	
Tanaidaceans									0.2 (0.2)	
Insects		0.2 (0.2)		1.1 (0.5)	0.1 (0.1)		0.8 (0.4)			
Bivalves		6.6 (3.2)	2.4 (0.9)	0.2 (0.1)	28.0 (3.7)	22.4 (9.4)	0.1 (0.1)	4.2 (1.4)	0.3 (0.2)	
Other	0.1 (0.1)					0.3 (0.2)	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)	
Total	0.8 (0.4)	16.1 (5.3)	39.0 (2.8)	3.3 (1.1)	59.1 (6.2)	58.2 (10.1)	4.0 (0.6)	37.0 (6.0)	53.1 (3.8)	

Table 6. Mean number of organisms per core from Area C microhabitats sampled in June 1973. Standard errors in parentheses. Nine cores were collected from each microhabitat: see Table 2 for abbreviations. Due to the scarcity of non-alga-covered mid tide and low tide emerged areas, cores used for those microhabitats were from substrate lightly covered by filamentous algae.

	<u>H Em</u>	<u>H Sa</u>	<u>H Su</u>	<u>M Em</u>	<u>M Sa</u>	<u>M Su</u>	<u>L Em</u>	<u>L Sa</u>	<u>L Su</u>
Annelids	(5)	(26)	(32)	(16)	(89)	(69)	(10)	(38)	(62)
Phyllodocids									
<u>Lumbrineris</u>		46	88	100	79	72	70	79	5
<u>Polydoris</u>	20	4			2	3	10	16	52
<u>Scoloplos</u>			3		10	25			40
<u>Streblospio</u>		8			3		10	3	3
<u>Capitella</u>	40	18			1				
<u>Mediomastus</u>	40	23	9		3				
<u>Notomastus</u>					1				
<u>Axiobella</u>							10		
Tube-dwelling Amphipods									
<u>Corophium (fused)</u>	(53)	(293)	(187)	(250)	(16)	(254)	(406)		
<u>Corophium stimpsoni</u>	96	66	100	99	100	98	79		
<u>Grandidierella</u>	4	32	1	1		2	21		
<u>Ampelisca</u>		2							T

Table 7. Percent composition of annelid and tube-dwelling amphipod species or species groups from June 1973 sampling of Area C. See Table 2 for abbreviations. Total numbers of annelids and amphipods in parentheses.

Mean Number / Core

(Standard Error)

	<u>H Em</u>	<u>H Sa</u>	<u>H Su</u>	<u>M Em</u>	<u>M Sa</u>	<u>M Su</u>	<u>L Em</u>	<u>L Su</u>
Nemerteans		0.7 (0.3)	1.0 (0.5)	0.4 (0.2)	0.2 (0.1)	0.7 (0.2)	0.7 (0.3)	1.0 (0.4)
Annelids	0.8 (0.4)	8.8 (1.3)	9.2 (0.8)	9.9 (0.8)	16.9 (2.2)	16.1 (3.1)	13.1 (0.9)	13.9 (1.7)
Tube-dwelling Amphipods		9.4 (3.8)	29.2 (6.1)	4.6 (1.6)	42.9 (6.6)	40.4 (6.5)	43.6 (5.7)	50.1 (5.6)
Tanaidaceans						0.1 (0.1)	0.1 (0.1)	0.2 (0.1)
Insects	9.7 (4.5)	0.4 (0.2)						
Bivalves			4.6 (2.8)	0.2 (0.1)	12.1 (3.0)	0.3 (0.2)	5.7 (2.1)	2.4 (0.9)
Other		0.2 (0.1)	0.1 (0.1)		0.1 (0.1)			0.2 (0.1)
Total	10.4 (4.4)	19.6 (4.8)	44.1 (5.6)	15.1 (2.3)	72.2 (9.8)	57.7 (8.2)	63.1 (6.1)	67.9 (5.1)

Table 8. Mean number of organisms per core from Area D microhabitats sampled in June 1973. Standard errors in parentheses. Nine cores were collected from each microhabitat: see Table 2 for abbreviations.

	<u>H Em</u>	<u>H Sa</u>	<u>H Su</u>	<u>M Em</u>	<u>M Sa</u>	<u>M Su</u>	<u>L Em</u>	<u>L Su</u>
Annelids	(7)	(79)	(83)	(89)	(152)	(145)	(118)	(125)
<u>Nephtys</u>					1		1	
<u>Lumbrineris</u>	57	72	92	74	75	50	68	70
<u>Polydorids</u>	14	4			11	34	14	8
<u>Scoloplos</u>			5	2		4	2	2
<u>Capitella</u>				1				
<u>Mediomastus</u>	29	3	2	15	1	7	13	1
<u>Notomastus</u>		18	2	8	11	6	3	18
<u>Axiiothella</u>		4			1			1
Bivalves			(41)	(2)	(109)	(3)	(51)	(22)
<u>Gemma</u>			100	50				
<u>Transennella</u>				50	100	100	100	95
<u>Protothaca</u>								5

Table 9. Percent composition of annelid and bivalve species or species groups from June 1973 sampling of Area D: see Table 2 for abbreviations. Total numbers of annelids and bivalves found in parentheses.

	Mean Number / Core						
	(Standard Error)						
	<u>H Em</u>	<u>H Sa</u>	<u>H Su</u>	<u>M Em</u>	<u>M Su</u>	<u>L Em</u>	<u>L Su</u>
Nemerteans			0.3 (0.2)			0.3 (0.2)	0.3 (0.2)
Annelids	0.7 (0.4)	1.8 (0.7)	2.6 (0.8)	0.1 (0.1)	2.3 (0.6)	1.8 (0.6)	1.0 (0.6)
Sand-dwelling Amphipods	2.8 (1.0)	0.2 (0.1)				0.2 (0.1)	0.2 (0.6)
Tube-dwelling Amphipods	5.1 (2.8)	0.1 (0.1)				1.8 (0.6)	
Tanaidaceans		0.1 (0.1)	0.2 (0.2)				
Holothuroideans							1.0 (0.4)
Other				0.1 (0.1)	0.1 (0.1)		
Total	8.6 (2.9)	2.2 (0.9)	3.1 (0.9)	0.2 (0.1)	2.4 (0.6)	4.1 (1.0)	2.6 (0.6)

Table 10. Mean number of organisms per core from Area E microhabitats sampled in June 1973. Standard errors in parentheses. Nine cores were collected from each microhabitat: see Table 1 for abbreviations.

	<u>H Em</u>	<u>H Sa</u>	<u>H Su</u>	<u>M Em</u>	<u>M Su</u>	<u>L Em</u>	<u>L Su</u>
Annelids	(6)	(16)	(23)	(1)	(21)	(16)	(9)
Unidentified			17	100	71	12	
Eteone		6					
Glycinde	67		13			25	11
Glycerid							11
Hemipodus			9				
Scoloplos		6	4				
Polydorids		17	25				
Scololepis		6	30		24		
Magelona		6					
Ophelia							22
Mediomastus	177	44	26		5	50	56
Notomastus		6				12	

Table 11. Percent composition of annelid species or species groups from June 1973 sampling of Area E: see Table 2 for abbreviations. Total number of annelids found in parentheses.

	Mean Number / Core						
	(Standard Error)						
	<u>H Em</u>	<u>H Sa</u>	<u>H Su</u>	<u>M Em</u>	<u>M Su</u>	<u>L Em</u>	<u>L Su</u>
Anthozoans		0.1 (0.1)	0.2 (0.1)	2.2 (0.5)	5.3 (1.9)	2.4 (1.0)	2.1 (1.1)
Nemerteans			0.3 (0.2)		0.7 (0.3)	0.9 (0.4)	0.8 (0.4)
Annelids	0.1 (0.1)	12.8 (3.6)	31.4 (10.2)	4.0 (0.9)	11.4 (1.8)	4.9 (1.3)	2.9 (1.1)
Alga-dwelling Amphipods	0.3 (0.2)	0.2 (0.1)	0.3 (0.2)	0.1 (0.1)	0.1 (0.1)		0.6 (0.4)
Tube-dwelling Amphipods	0.1 (0.1)		0.6 (0.3)		0.6 (0.2)	1.2 (0.4)	0.3 (0.2)
Insects	5.3 (1.4)	3.3 (1.0)	0.6 (0.2)				
Bivalves			0.1 (0.1)	5.3 (1.3)	12.8 (5.9)	13.7 (2.7)	14.7 (3.4)
Other	0.2 (0.1)						0.2 (0.1)
Total	6.1 (1.4)	16.4 (4.2)	33.6 (10.1)	11.7 (1.4)	30.9 (6.9)	23.1 (3.4)	21.6 (2.9)

Table 12. Mean number of organisms per core from Area A microhabitats sampled in December 1973. Standard errors in parentheses. Nine cores were collected from each microhabitat: see Table 2 for abbreviations.

	<u>H Em</u>	<u>H Sa</u>	<u>H Su</u>	<u>M Em</u>	<u>M Su</u>	<u>L Em</u>	<u>L Su</u>
Annelids	(1)	(115)	(283)	(36)	(103)	(44)	(26)
<u>Eteone</u>		1	2		2		4
<u>Lumbrineris</u>	100						
<u>Polydorids</u>		98	59	81	44	64	35
<u>Streblospio</u>		1	32		14	2	4
<u>Capitella</u>			7	19	41	34	54
<u>Notomastus</u>							4
Alga-dwelling Amphipods	(3)	(2)	(3)	(1)	(1)	(0)	(5)
<u>Allorchestes</u>	67						
<u>Ampithoe</u>		50	33				
<u>Anisogammarus</u>	33	50	67	100	100		100
Tube-dwelling Amphipods	(1)	(0)	(5)	(0)	(5)	(11)	(0)
<u>Corophium</u>	100		40			27	
<u>C. stimpsoni</u>					60	27	
<u>C. spinicorne</u>			60				
<u>Grandidierella</u>					40	36	
<u>Ampelisca</u>						9	

Table 13. Percent composition of annelid, alga-dwelling amphipod, and tube-dwelling amphipod species or species groups from December 1973 sampling of Area A. See Table 2 for abbreviations. Total numbers of annelids and amphipods in parentheses.

	Mean Number / Core									
	(Standard Error)									
	<u>H Em</u>	<u>H Sa</u>	<u>H Su</u>	<u>M Em</u>	<u>M Sa</u>	<u>M Su</u>	<u>L Em</u>	<u>L Sa</u>	<u>L Su</u>	
Nemertean		1.0 (0.5)	0.3 (0.2)	0.7 (0.3)	0.6 (0.2)	0.9 (0.4)	0.3 (0.2)	0.4 (0.2)	0.9 (0.3)	
Annelids	0.4 (0.3)	3.9 (0.8)	7.9 (1.2)	8.3 (1.0)	9.1 (0.7)	5.8 (1.4)	11.4 (4.5)	11.8 (3.2)	10.7 (2.8)	
Alga-dwelling Amphipods	0.9 (0.8)							0.1 (0.1)	0.2 (0.2)	
Tube-dwelling Amphipods		1.3 (0.9)	8.3 (1.6)	9.8 (2.7)	4.9 (1.4)	7.9 (2.3)	4.7 (0.9)	11.1 (3.5)	3.3 (1.1)	
Tanaidaceans		0.1 (0.1)	0.2 (0.2)	0.1 (0.1)	0.1 (0.1)	0.8 (0.4)	16.4 (9.2)	26.7 (14.9)	9.8 (3.9)	
Insects	8.2 (2.3)	0.2 (0.1)								
Bivalves		0.3 (0.2)	1.4 (0.5)	0.4 (0.3)	0.6 (0.3)		3.4 (1.8)	4.9 (1.9)	1.9 (1.3)	
Other	0.2 (0.2)								0.3 (0.2)	
Total	9.9 (2.6)	6.9 (1.5)	19.3 (2.7)	19.3 (2.8)	15.2 (1.8)	15.3 (3.5)	36.3 (9.2)	55.0 (17.0)	27.1 (6.9)	

Table 14. Mean number of organisms per core from Area D microhabitats sampled in December 1973. Standard errors in parentheses. Nine cores were collected from each microhabitat: see Table 2 for abbreviations.

	<u>H Em</u>	<u>H Sa</u>	<u>H Su</u>	<u>M Em</u>	<u>M Sa</u>	<u>M Su</u>	<u>L Em</u>	<u>L Sa</u>	<u>L Su</u>
Annelids									
Unidentified	(4)	(35)	(71)	(75)	(82)	(52)	(103)	(106)	(96)
Nereid		3					1		1
Glycinde			4	3		2	3	2	1
Nephtys									1
Lumbrineris	75	54	45	55	67	54	31	35	59
Scoloplos									1
Polydorids			7		4	2	54	24	12
Armandia		3	11	1	7	25		15	11
Mediomastus		29	30	39	20	13	11	16	12
Notomastus	25	11	3	3	2	4		8	
Alga-dwelling Amphipods	(8)							(1)	(2)
Unidentified									50
Allorchestes	12								
Ampithoe	88							100	
Anisogammarus									50
Tube-dwelling Amphipods		(12)	(75)	(88)	(44)	(71)	(42)	(99)	(30)
Corophium (fused)		100	100	100	100	100	100	98	83
Grandidierella								2	17

Table 15. Percent composition of annelid and alga-dwelling and tube-dwelling amphipod species and species groups from December 1973 sampling of Area D. See Table 2 for abbreviations. Total numbers of annelids and amphipods found in parentheses.

	Mean Number / Core					
	(Standard Error)					
	<u>H Em</u>	<u>H Su</u>	<u>M Em</u>	<u>M Su</u>	<u>L Em</u>	<u>L Su</u>
Nemerteans						0.1 (0.1)
Annelids	2.0 (0.6)	1.8 (0.3)	0.7 (0.3)	1.6 (0.7)	1.4 (0.4)	1.6 (0.6)
Sand-dwelling Amphipods	14.8 (3.2)	9.9 (3.1)	0.6 (0.3)	0.4 (0.3)		
Alga-dwelling Amphipods						0.2 (0.1)
Tube-dwelling Amphipods					0.1 (0.1)	
Tanaidaceans						0.7 (0.5)
Other					0.1 (0.1)	
Total	16.8 (3.3)	11.7 (3.1)	1.4 (0.4)	2.0 (0.9)	1.7 (0.4)	2.6 (0.9)

Table 16. Mean number of organisms per core from Area E microhabitats sampled in December 1973. Standard errors in parentheses. Nine cores were collected from each microhabitat: see Table 2 for abbreviations.

	<u>H Em</u>	<u>H Su</u>	<u>M Em</u>	<u>M Su</u>	<u>L Em</u>	<u>L Su</u>
Annelids	(18)	(16)	(6)	(14)	(13)	(14)
Unidentified	72	56	67	36		
<u>Glycinde</u>	11	25			8	
<u>Glycerid</u>						7
<u>Nephtys</u>			17	7		
<u>Scololepis</u>			17			
<u>Armandia</u>					8	14
<u>Ophelia</u>					46	43
<u>Mediomastus</u>		6		57	8	
<u>Notomastus</u>	17	12			23	29
<u>Polycirrus</u>					8	7

Table 17. Percent composition of annelid species or species groups from December 1973 sampling of Area E. See Table 2 for abbreviations. Total number of annelids found in parentheses.

	Mean Number / Core					
	(Standard Error)					
	<u>H Em</u>	<u>H Sa</u>	<u>H Su</u>	<u>L Em</u>	<u>L Sa</u>	<u>L Su</u>
Number of cores	25	10	17	13	22	25
Nemerteans	0.1 (0.1)	0.1 (0.1)	0.4 (0.1)	1.3 (0.8)	0.5 (0.2)	0.3 (0.2)
Annelids	0.7 (0.2)	3.2 (1.3)	3.7 (0.6)	3.8 (1.1)	5.0 (0.7)	5.5 (0.9)
Alga-dwelling Amphipods	T	0.0	0.0	0.0	0.5 (0.3)	0.4 (0.1)
Tube-dwelling Amphipods	3.2 (1.9)	9.7 (3.9)	21.3 (4.0)	22.1 (4.7)	24.2 (4.7)	33.2 (4.3)
Tanaidaceans	0.0	0.0	0.0	0.0	0.1 (0.1)	0.8 (0.5)
Insects	0.6 (0.2)	0.1 (0.1)	0.0	0.1 (0.1)	0.0	0.0
Bivalves	0.3 (0.2)	5.0 (2.8)	10.4 (4.0)	1.6 (0.7)	5.3 (1.8)	3.2 (2.4)
Total	5.1 (2.1)	18.4 (7.4)	36.3 (6.8)	28.4 (5.6)	35.7 (5.1)	43.4 (4.9)

Table 18. Mean number of organisms per core from non-alga-covered microhabitats of the Invertebrate Sampling Plot, July through October 1973. High cores taken from stations 1-14, low cores from stations 15-28. Standard errors in parentheses. See Table 2 for abbreviations. For very small values, $0.00 < T < 0.05$.

	Mean Number / Core					
	(Standard Error)					
	<u>H Em</u>	<u>H Sa</u>	<u>H Su</u>	<u>L Em</u>	<u>L Sa</u>	<u>L Su</u>
Number of cores	60	19	30	34	30	45
Nemerteans	0.6 (0.2)	0.4 (0.2)	0.1 (0.1)	0.2 (0.1)	0.1 (0.1)	0.2 (0.1)
Annelids	5.1 (0.8)	12.7 (2.5)	12.3 (1.9)	5.9 (0.7)	8.9 (0.9)	8.4 (0.8)
Alga-dwelling Amphipods	T	0.0	0.1 (0.1)	0.0	0.1 (0.1)	T
Tube-dwelling Amphipods	1.1 (0.3)	5.4 (1.2)	6.8 (0.9)	3.9 (0.7)	5.3 (0.9)	6.1 (0.8)
Tanaidaceans	0.0	0.1 (0.1)	0.0	0.1 (0.1)	1.1 (0.5)	3.8 (1.5)
Insects	0.8 (0.1)	0.1 (0.1)	0.0	0.0	0.0	0.0
Bivalves	0.1 (T)	2.6 (1.0)	7.5 (1.7)	0.5 (0.2)	3.1 (1.1)	2.4 (0.8)
Total	7.9 (0.9)	21.5 (2.8)	27.1 (2.9)	10.6 (1.1)	18.6 (2.1)	20.8 (1.8)

Table 19. Mean number of organisms per core from non-alga-covered microhabitats of the Invertebrate Sampling Plot, December 1973 through February 1974. High cores taken from stations 1-14, low cores from stations 15-28. Standard errors in parentheses. See Table 2 for abbreviations. For very small values, $0.00 < T < 0.05$.

	Mean Number / Core					
	(Standard Error)					
	<u>H Em</u>	<u>H Sa</u>	<u>H Su</u>	<u>L Em</u>	<u>L Sa</u>	<u>L Su</u>
Number of cores	37	8	25	27	29	28
Nemerteans	0.4 (0.1)	0.4 (0.2)	0.2 (0.1)	0.1 (0.1)	0.2 (0.1)	0.3 (0.1)
Annelids	4.8 (1.0)	6.2 (2.4)	6.1 (1.3)	4.3 (0.7)	5.2 (0.7)	6.1 (1.2)
Alga-dwelling Amphipods	0.1 T	0.0	0.2 (0.2)	0.0	0.0	0.0
Tube-dwelling Amphipods	2.5 (0.8)	2.0 (1.0)	3.8 (1.0)	0.7 (0.3)	8.1 (1.6)	10.5 (2.4)
Tanaidaceans	T	0.0	0.0	T	1.7 (0.5)	4.8 (1.7)
Insects	1.8 (0.9)	0.2 (0.2)	0.4 (0.4)	0.0	0.0	0.0
Bivalves	0.6 (0.3)	0.1 (0.1)	0.8 (0.2)	0.1 (0.1)	0.6 (0.2)	0.4 (0.2)
Total	10.4 (1.7)	9.1 (3.3)	11.6 (2.0)	5.3 (0.8)	15.9 (1.8)	22.2 (3.1)

Table 20. Mean number of organisms per core from non-alga-covered microhabitats of the Invertebrate Sampling Plot, March through May 1973. High cores taken from stations 1-14, low cores from stations 15-28. Standard errors in parentheses. See Table 2 for abbreviations. For very small values, $0.00 < T < 0.05$.

	<u>No Dif-</u> <u>ference</u>	<u>S>D</u>	<u>S>E</u>	<u>D>E</u>	<u>D>S</u>	<u>E>S</u>	<u>E>D</u>	<u>Number of 2-way</u> <u>Comparisons</u>
High & Mid Tide Zones								
Nemerteans	21		1					22
Annelids	26		11	8	1	1		47
Tube-dwelling Amphipods	21	5	12	6				44
Insects	12				1	6	2	21
Bivalves	20	3	7	4	1	2	1	38
Total Organisms	25	5	12	4		1		47
Low Tide Zone								
Nemerteans	8							8
Annelids	20			1				21
Tube-dwelling Amphipods	16		1	2		1		20
Tanaidaceans	9							12
Bivalves	15		2	3	1			18
Total Organisms	15		3	3				21

Table 21. Frequencies of significant differences between the densities of organisms in different microhabitats. All comparisons made within each tide zone. S is submerged, D is saturated, E is emerged. Data include June and December 1973 core samples from areas A, B, C, D, and E and July 1973 through May 1974 core samples from the ISP high tide zone (included in High & Mid Tide Zones) and Low Tide Zone. Densities were considered significantly different when means + or - 2 standard errors did not overlap.

Area	Micro-habitat	Alga Type	Alga-covered Cores				Non-alga-covered cores				Diff.
			Algal Weight	Number	Percent of Total	<u>All. Amp. Ani.</u>	AdA/core	Number	Percent of Total	<u>All. Amp. Ani.</u>	
A	M Em	F 6	0.4 (0.1)	5.7 (3.1)	9	71	21	0.2 (0.2)	100	NS	
C	M Em	F 6	1.4 (0.2)	0.7 (0.7)	100			0.0		NS	
C	H Su	F 9	-	4.0 (2.2)	89	11		0.1 (0.1)	100	NS	
C	L Su	F 9	0.7 (0.1)	6.8 (3.1)	96	4		0.0		Sig.	
D	H Em	F 6	0.6 (0.1)	1.3 (1.2)	100			0.3 (0.3)	100	NS	
D	H Em	F 6	0.6 (0.1)	1.3 (1.2)	100			0.3 (0.3)	100	NS	
D	L Em	F 6	0.6 (0.2)	16.3 (8.7)	100			0.0		NS	
D	H Sa	F 9	0.7 (0.1)	0.0				0.0		NS	
A	L Su	B 6	0.8 (0.1)	47.3 (9.7)	8	76	15	0.8 (0.5)	100	Sig.	
C	L Su	B 6	0.9 (0.1)	47.5 (15.1)	93	4	3	0.0		Sig.	
D	L Su	B 6	0.8 (0.1)	36.0 (9.9)	90	2	8	0.3 (0.2)	100	Sig.	

Table 22. Comparison between the numbers of alga-dwelling amphipods found in alga-covered and non-alga-covered cores from three areas on Bolinas Lagoon in June - August 1973 and 1974. Area A is the muddiest, Area D the sandiest. Microhabitat abbreviations as in Table 2. Alga types are filamentous (F) and broad-bladed (B). Under algal weights and number of alga-dwelling amphipods (AdA) core are means above and standard errors, in parentheses, below. Amphipods are Allorchestes(All.), Ampithoe(Amp.), and Anisogammarus(Ani.). Differences (Diff.) between mean numbers of amphipods / core were significant (Sig.) if means + or - 2 standard errors did not overlap; otherwise means were not significantly different (NS).

	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
Nemertean	1.2	1.0	.4	0.5	1.4	1.2	2.5	2.4	1.9	1.6	2.1	2.7
Annelids	21.5	11.0	8.3	9.9	16.7	41.9	58.2	53.8	45.6	49.7	41.4	32.9
Alga-dwelling Amphipods	0.1	12.6	34.6	8.0	1.0	2.1	0.6	0.1	0.0	0.7	0.2	0.0
Tube-dwelling Amphipods	58.0	58.6	48.5	67.4	51.9	27.1	17.1	24.5	31.9	32.9	44.1	37.2
Leptochelia	2.9	0.7	0.1	0.2	1.5	3.2	2.3	8.2	8.5	10.6	6.9	9.4
Insects	3.3	0.4	0.4	0.3	0.5	2.9	0.6	1.4	0.6	0.4	2.1	9.7
Clams	12.2	15.5	7.6	13.6	26.4	21.5	17.9	9.2	10.9	3.7	2.6	7.0
Other	0.7	0.2	0.1	0.1	0.7	0.2	1.3	0.4	0.6	0.4	0.6	1.2
Total Organisms	688	1740	2820	2544	1108	939	772	837	1080	762	621	672

Table 23. Percent composition of tidal flat organisms in all cores (alga-covered and non-alga-covered) from the ISP, June 1973 - May 1974.

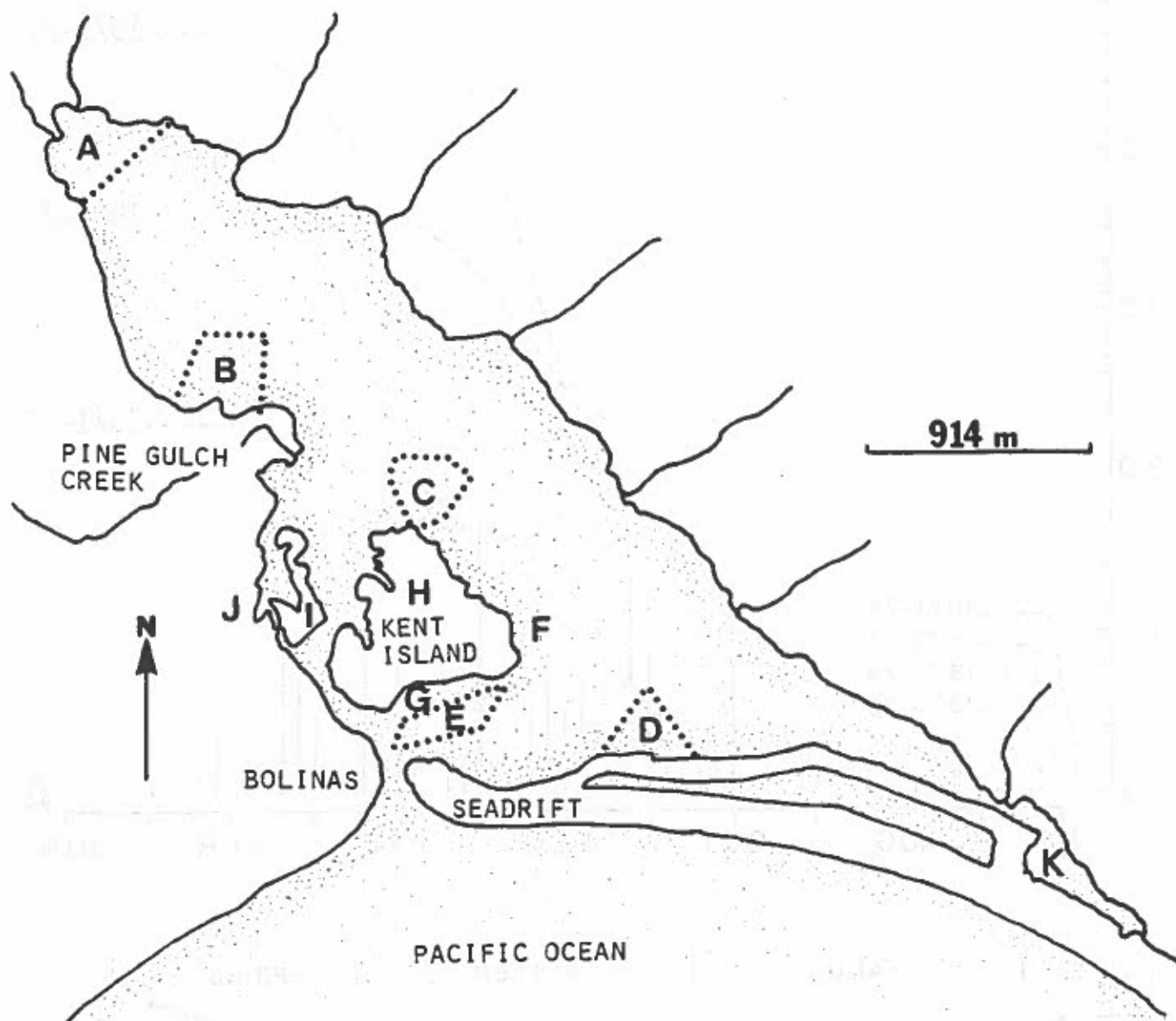


Figure 1. Drawing of Bolinas Lagoon. Areas A-E are the five areas of the tidal flat sampled; F, a roosting area on the tidal flat; G, the Kent Island sand beach; H, the Kent Island salt marsh; I, the Pine Gulch Creek delta salt marsh; J, abandoned fish ponds; and K, the mud flat high in the tidal zone at the south end of the estuary. Area A is approximately 12.6 hectares; B, 9.8 hectares; C, 8.0 hectares; D, 7.0 hectares; and E, 8.4 hectares.

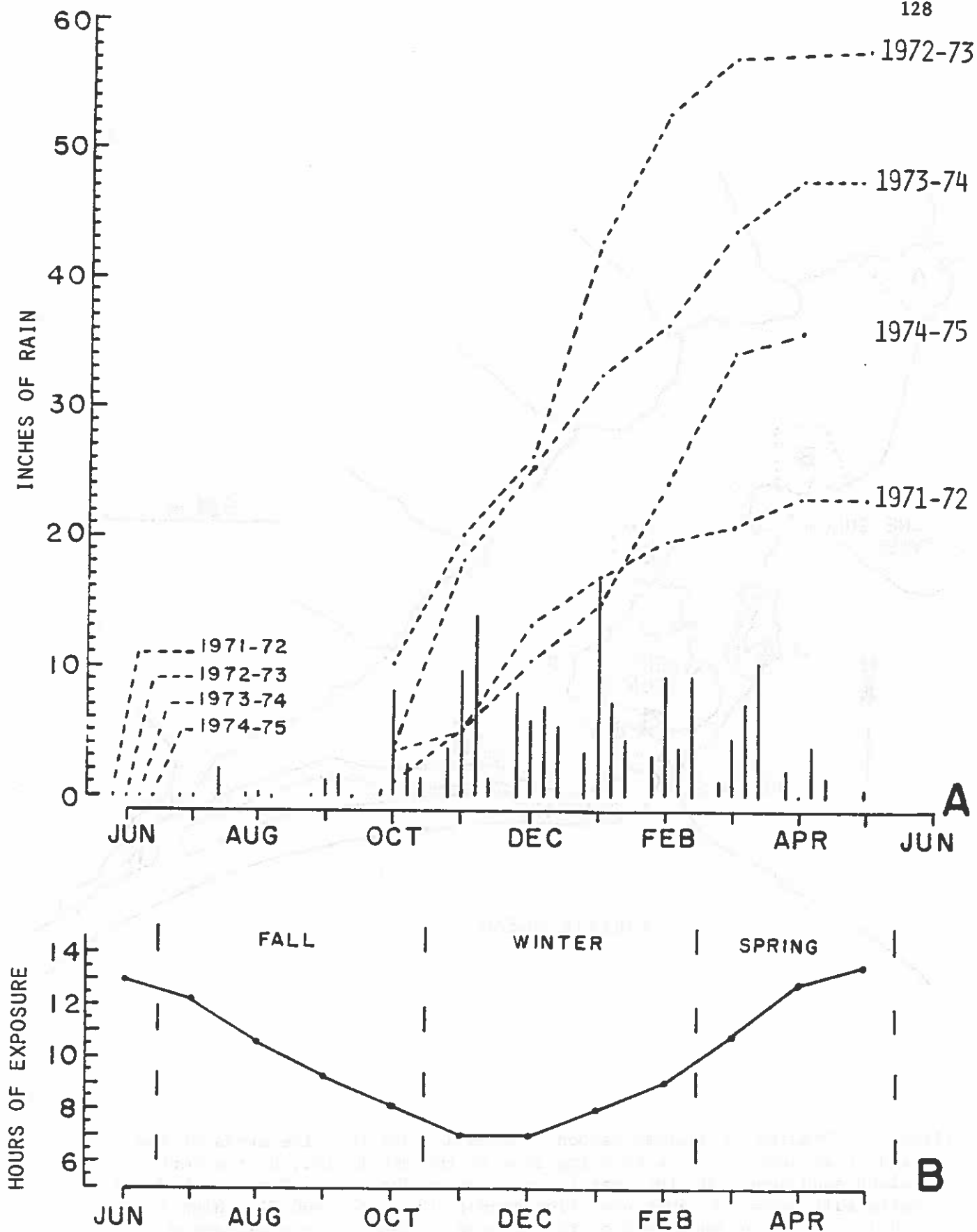


Figure 2. A: Monthly and cumulative rainfall at Bolinas, 1971-75. B: Average daytime exposure of tidal flat below 1.4 m above mean low water.

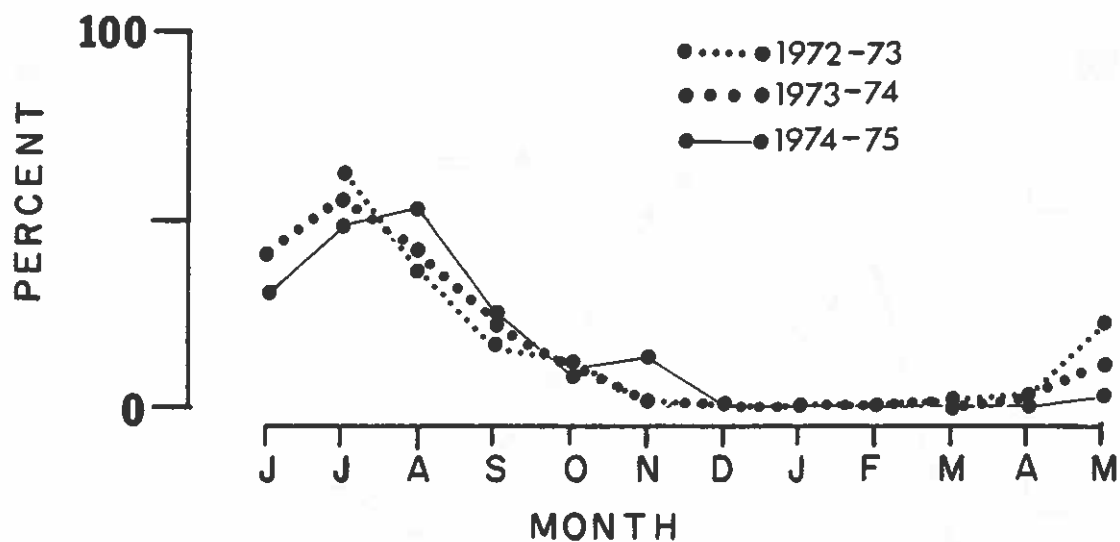


Figure 3. Percent of the ISP covered by algae at different times of year.

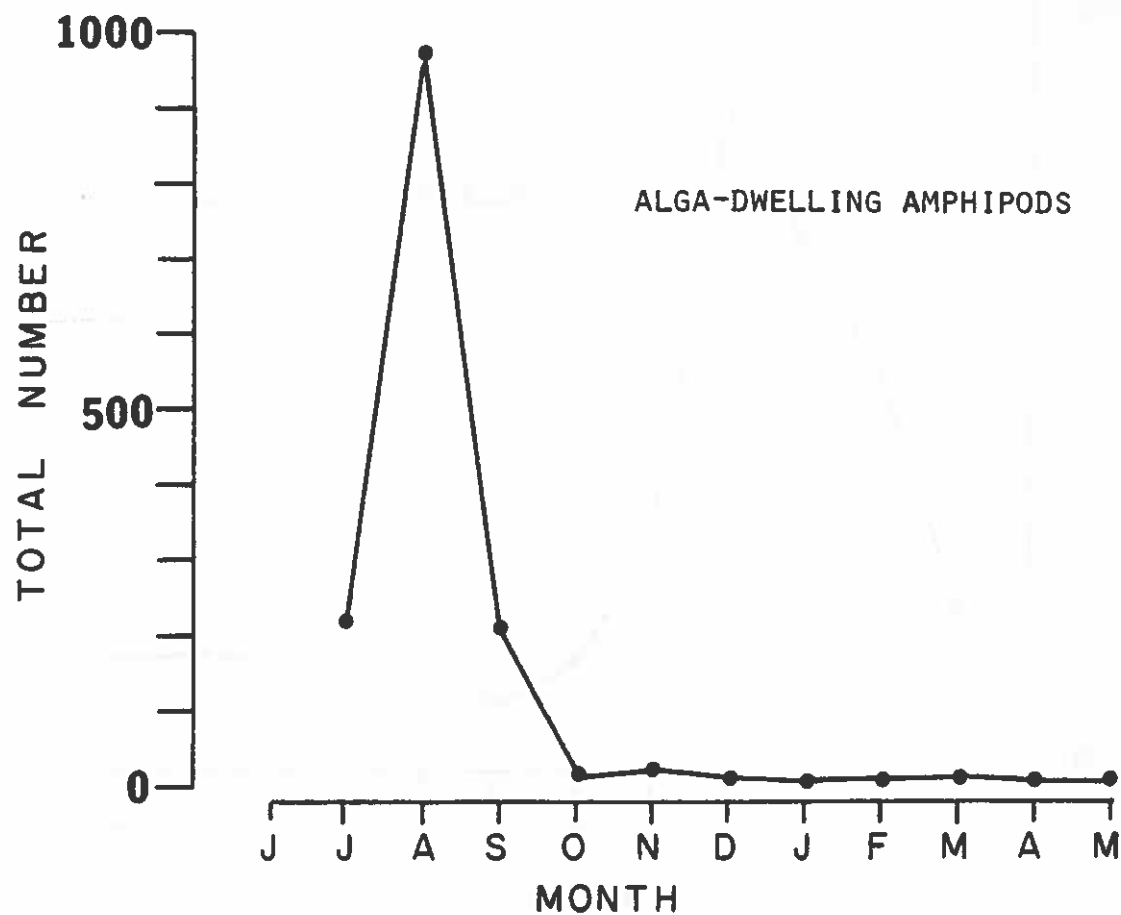


Figure 4. Total number of alga-dwelling amphipods in ISP cores each month.

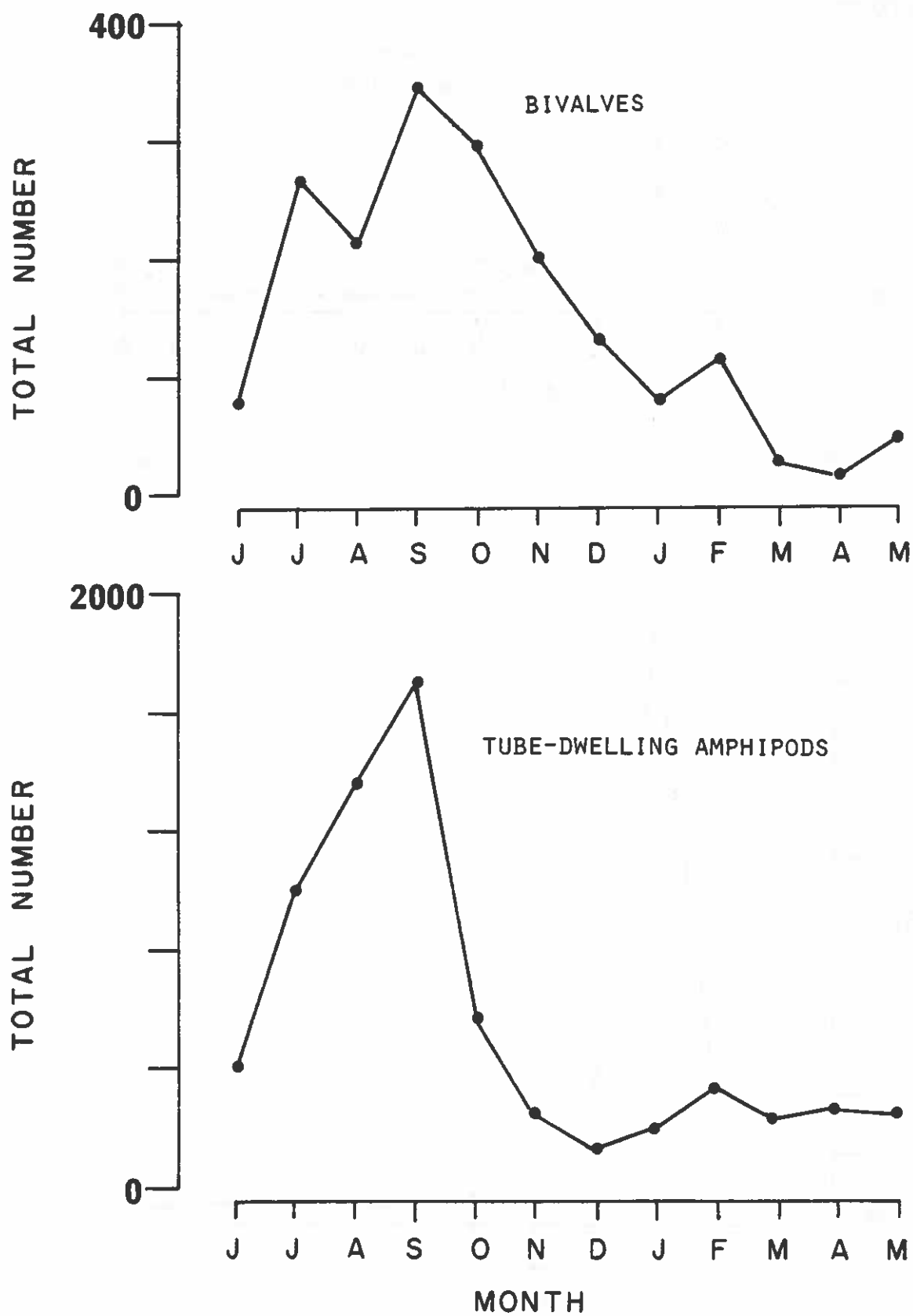


Figure 5. Total number of bivalves and tube-dwelling amphipods in ISP cores each month.

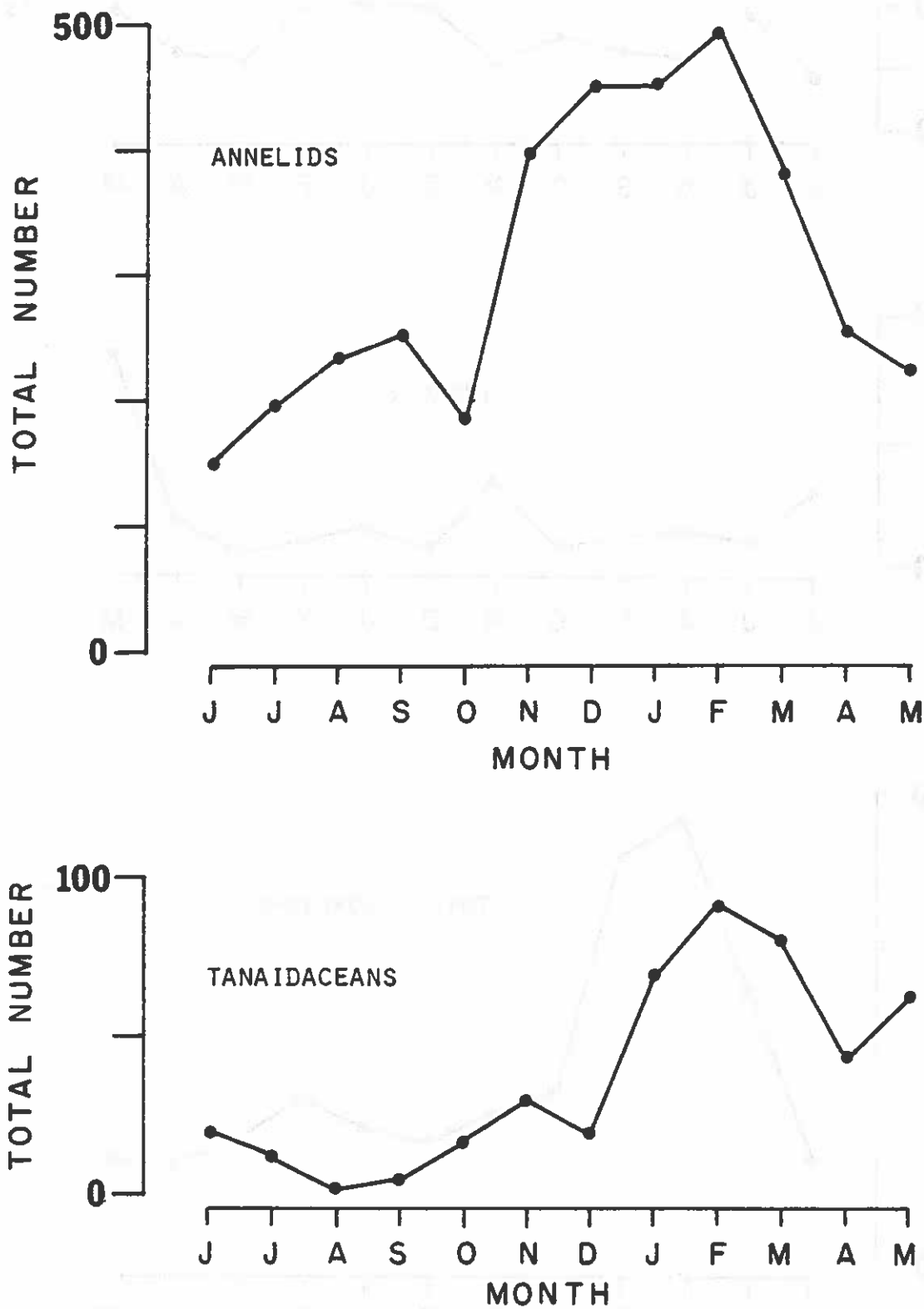


Figure 6. Total number of annelids and tanaidaceans in ISP cores each month.

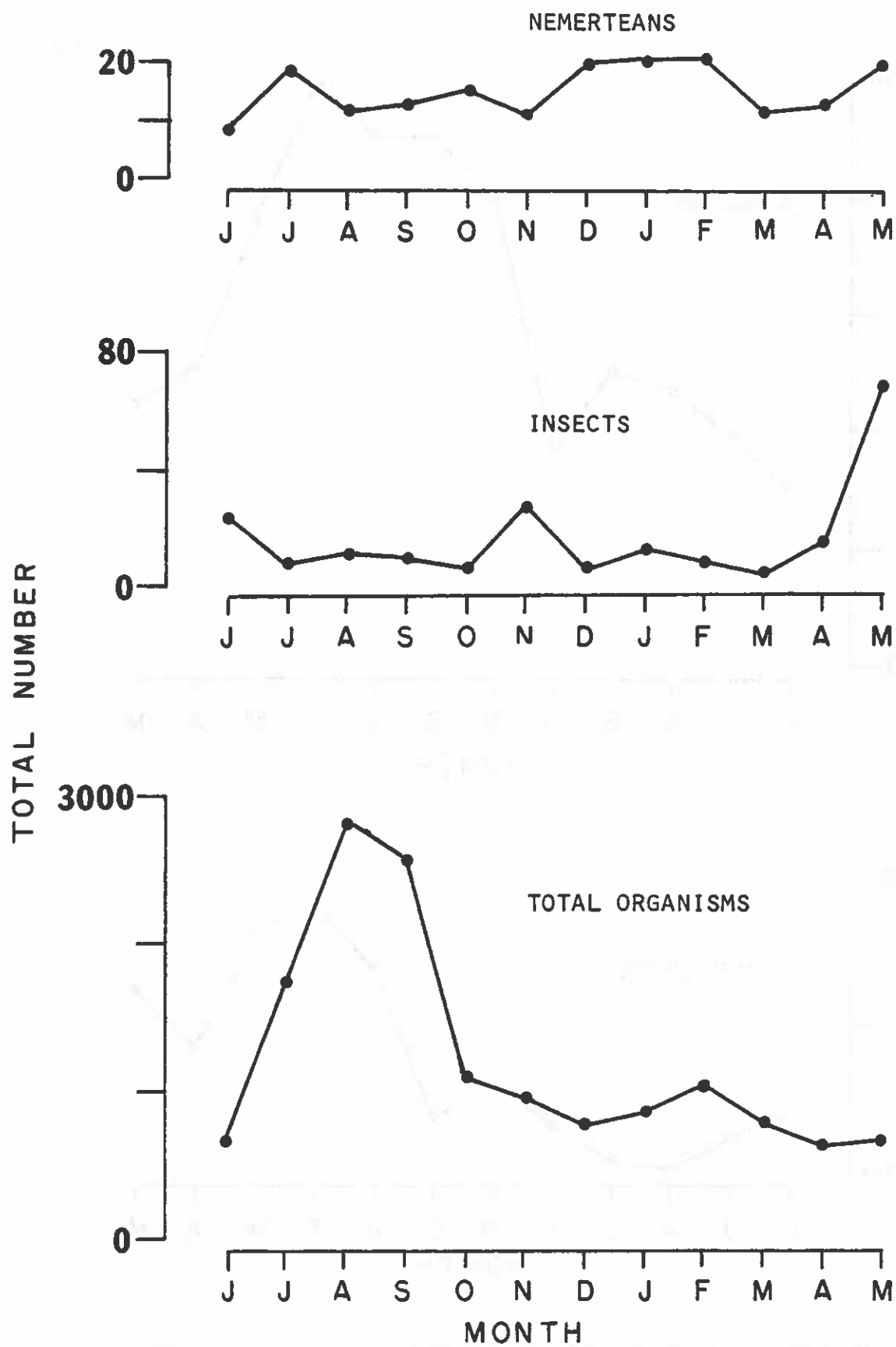


Figure 7. Total number of nemerteans, insects and all organisms combined in ISP cores each month.

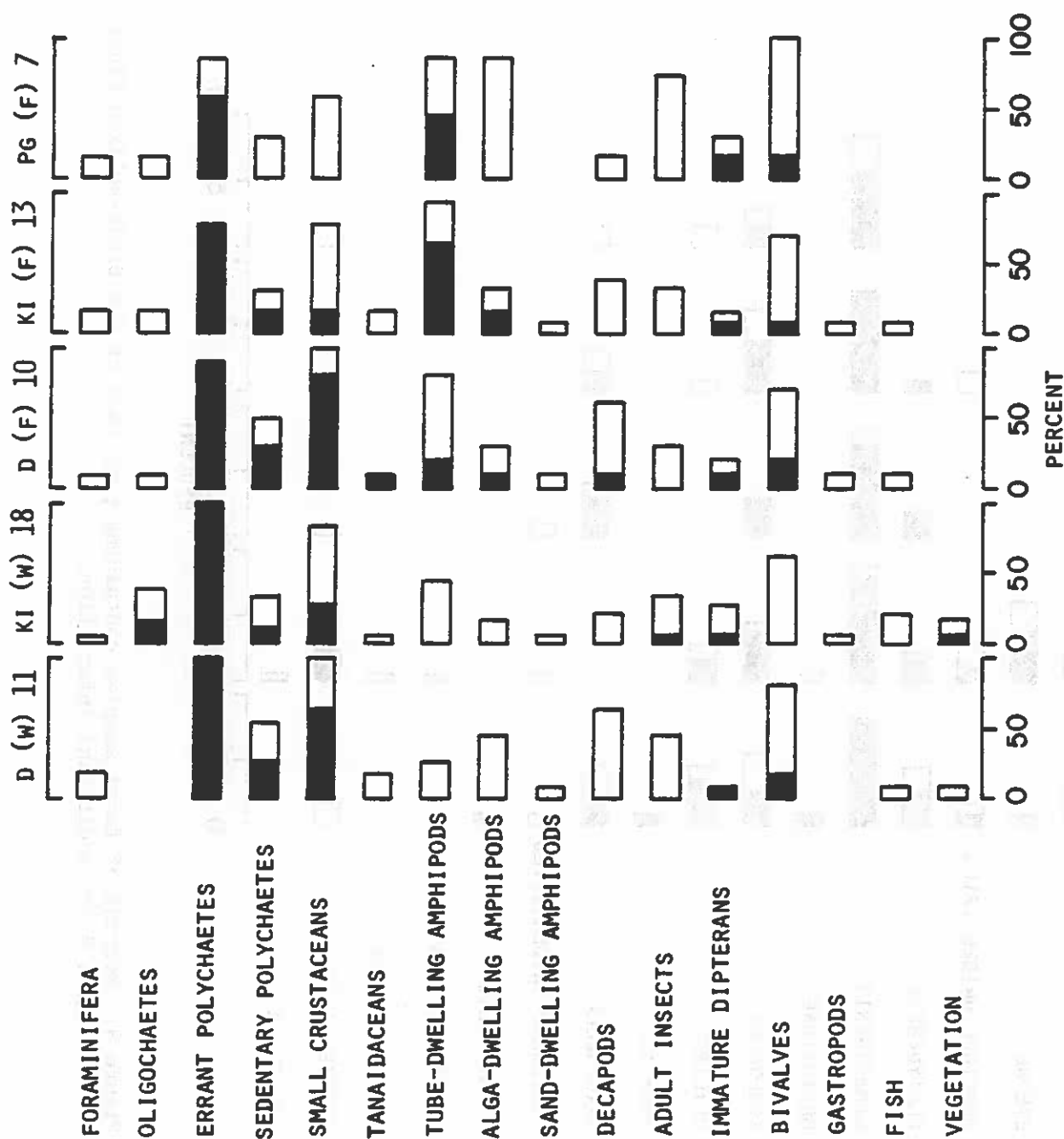


Figure 8. Percent of fecal samples containing each prey type of the Black-bellied Plover. KI is Kent Island and PG is Pine Gulch Creek delta; other letters outside parentheses are shown in Figure 1. Inside parentheses F is fall, W is winter and S is spring. The number of samples for each period follow the parentheses. A solid area indicates prey in primary amounts, an open area in trace amounts.

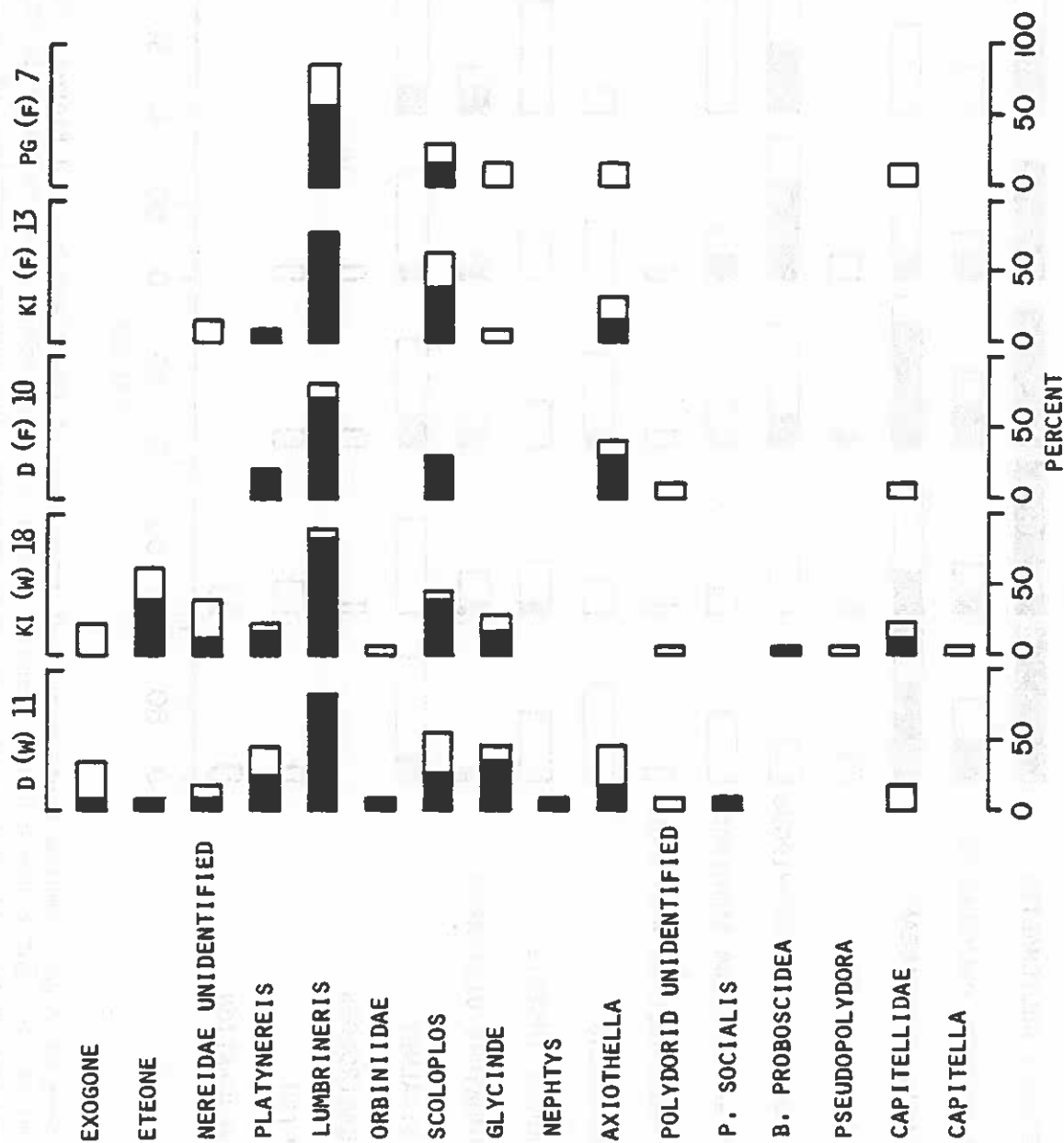


Figure 9. Percent of fecal samples containing prey taxa of the Black-bellied Plover. See Figure 8 for additional information.

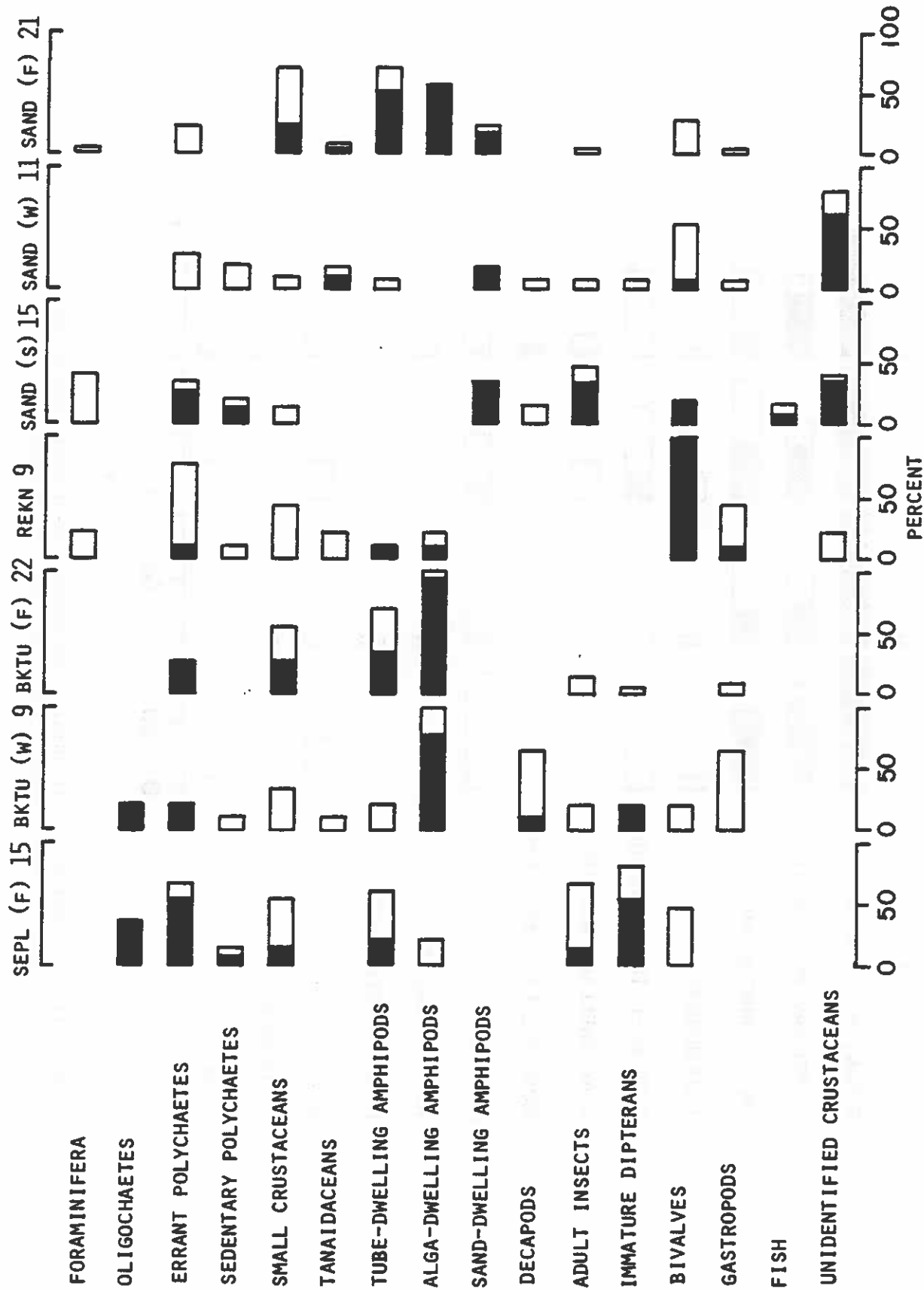


Figure 10. Percent of fecal samples containing each prey type of the Semipalmated Plover (SEPL), the Black Turnstone (BKTU), the Red Knot (REKN) and Sanderling (SAND). See Figure 8 for additional information.

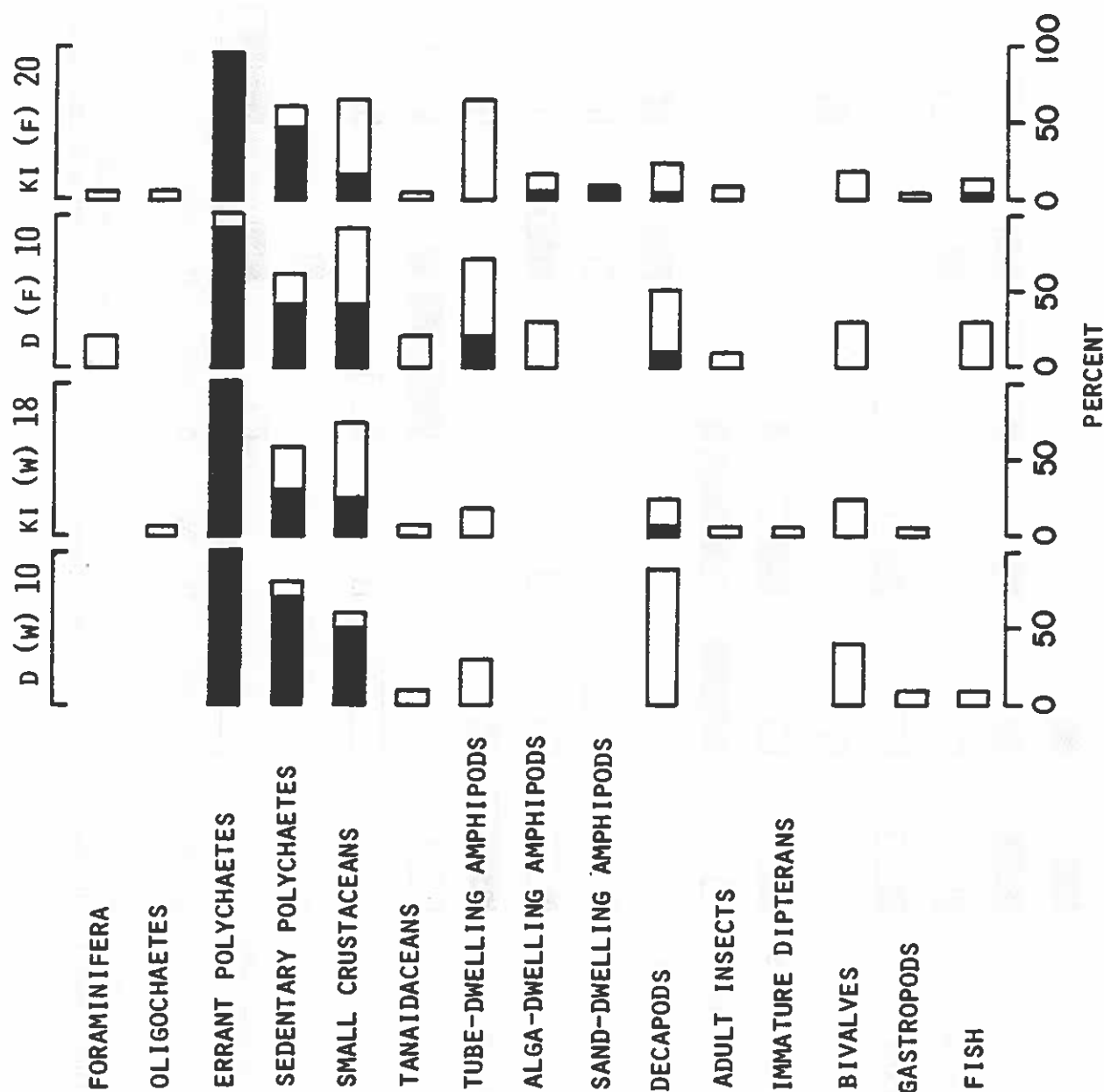


Figure 11. Percent of fecal samples containing each prey type of the Marbled Godwit. See Figure 8 for additional information.

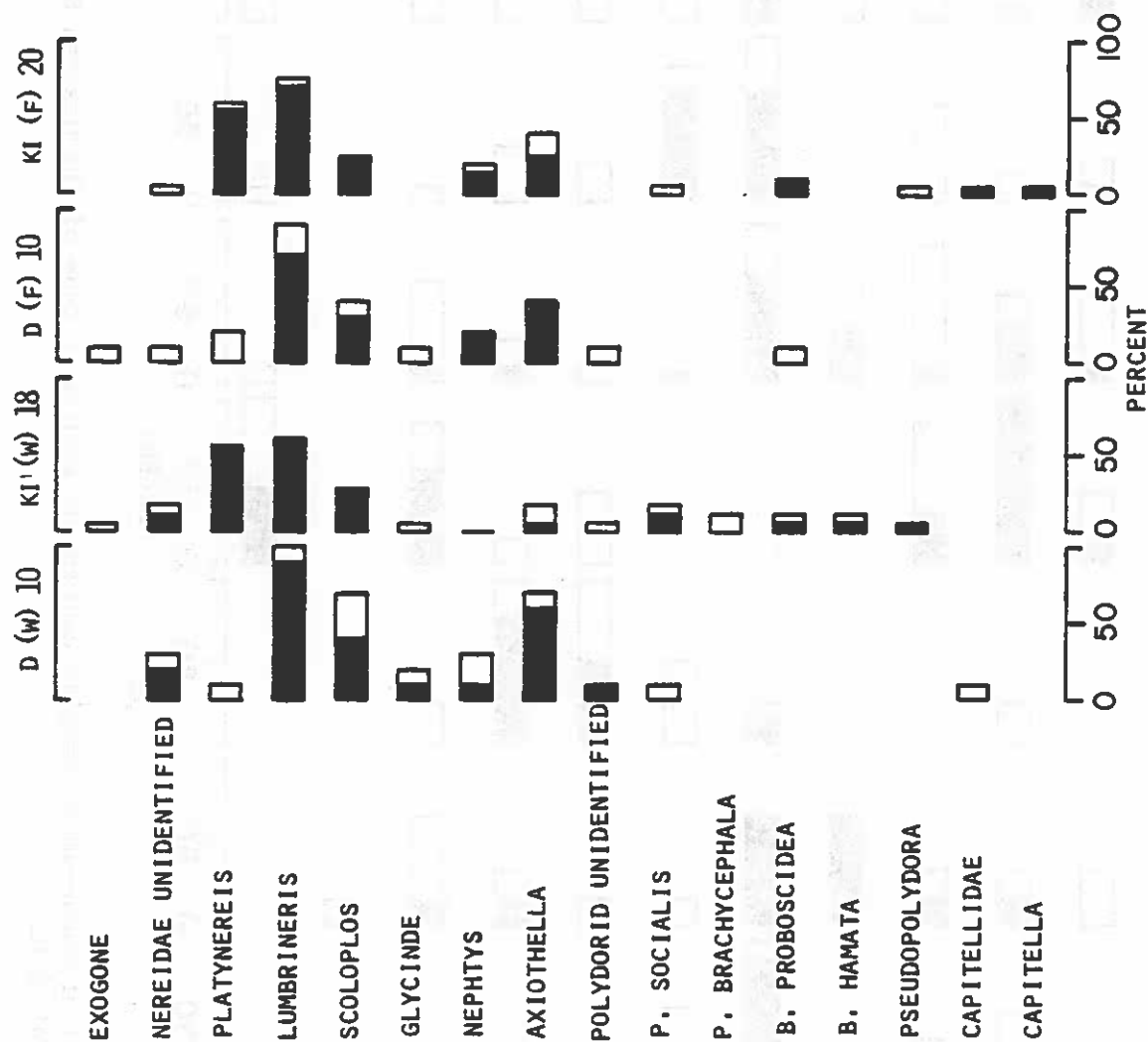


Figure 12. Percent of fecal samples containing prey taxa of the Marbled Godwit. See Figure 8 for additional information.

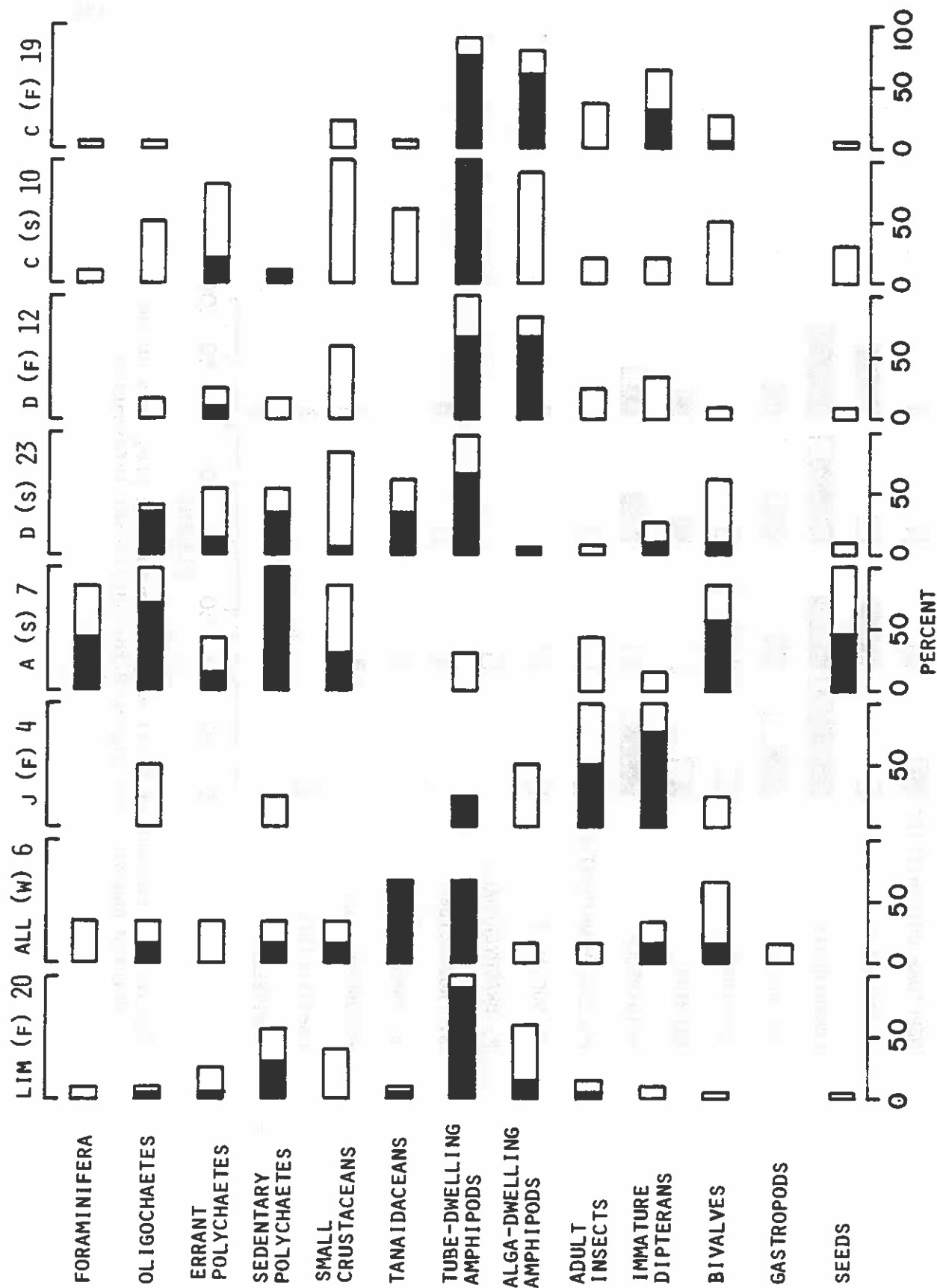


Figure 13. Percent of stomach-pumped samples containing each prey type of the Western Sandpiper. See Figure 8 for additional information.

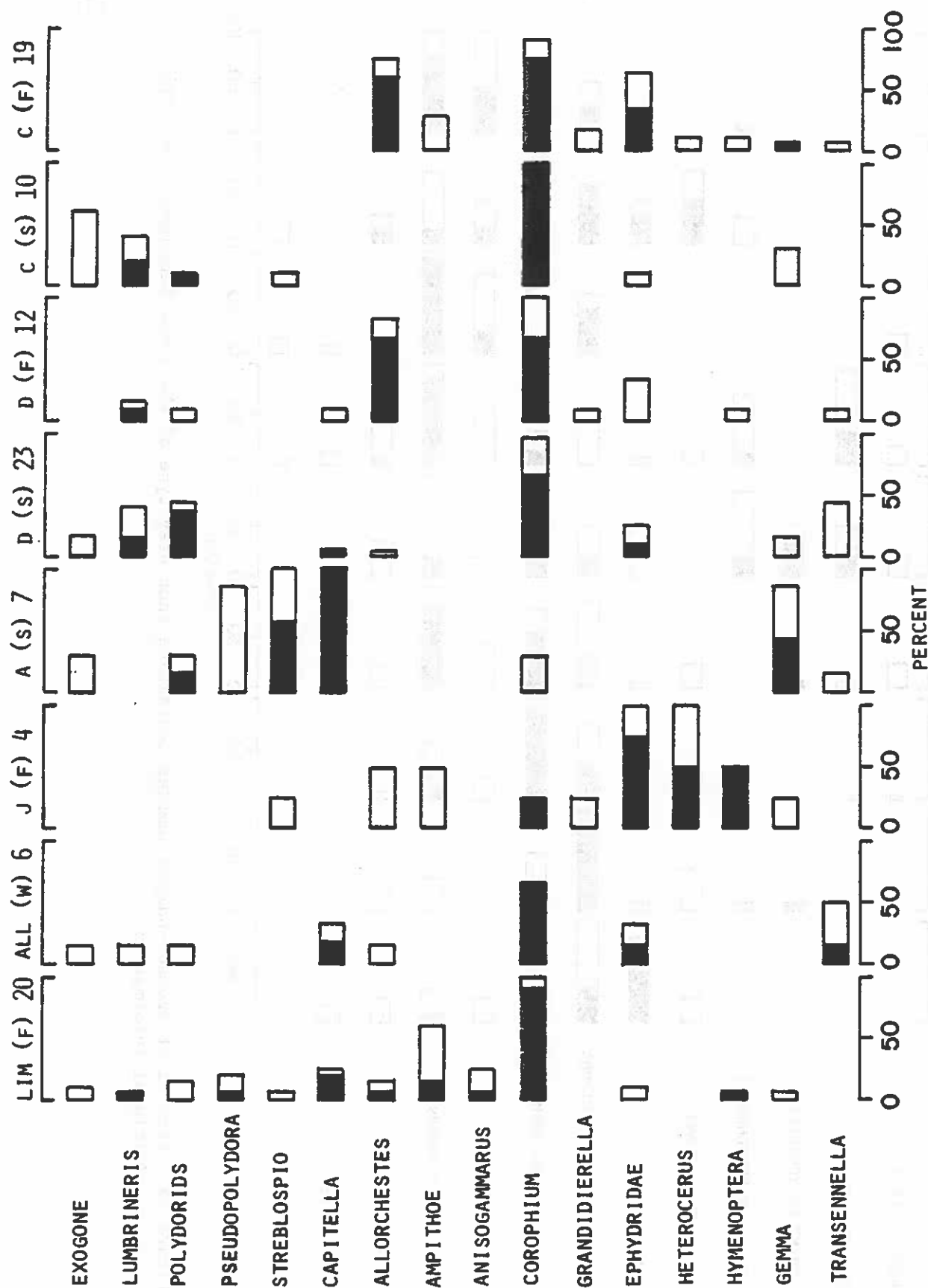


Figure 14. Percent of stomach-pumped samples containing prey taxa of the Western Sandpiper. LIM is Limantour Estero and ALL is all over Bolinas Lagoon. See Figure 8 for additional information.

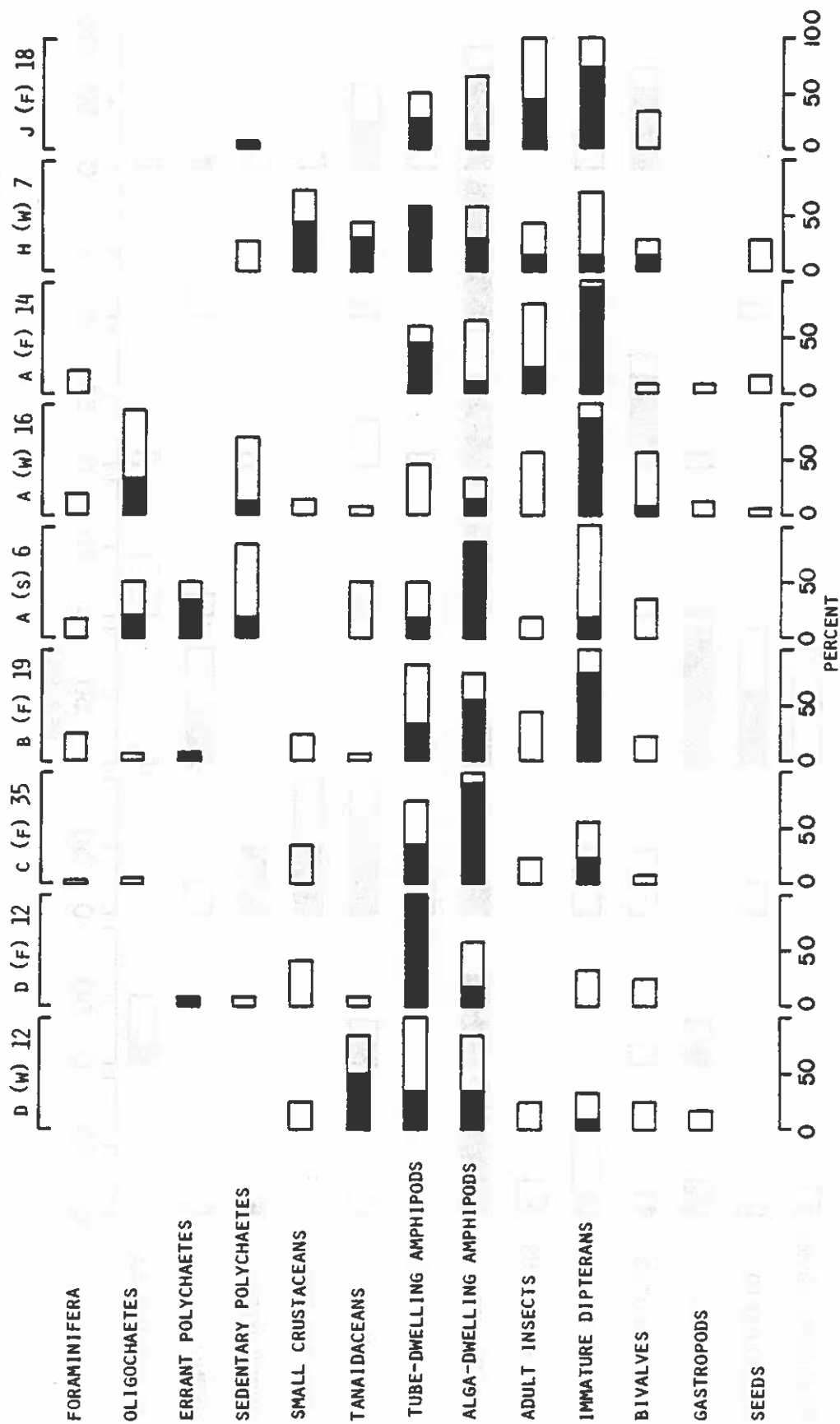


Figure 15. Percent of stomach-pumped samples containing each prey type of the Least Sandpiper. See Figure 8 for additional information.

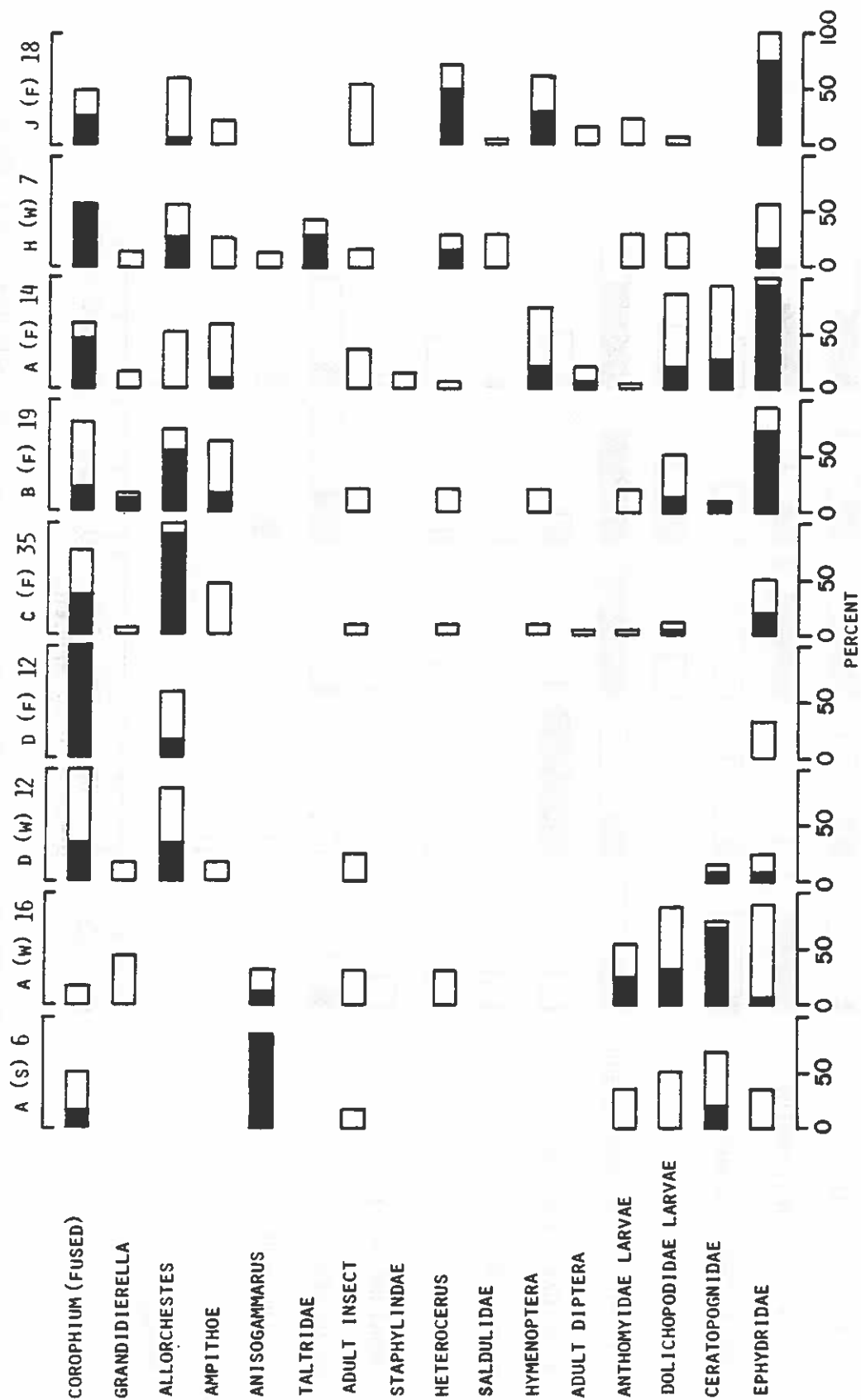


Figure 16. Percent of stomach-pumped samples containing prey taxa of the Least Sandpiper. See Figure 8 for additional information.

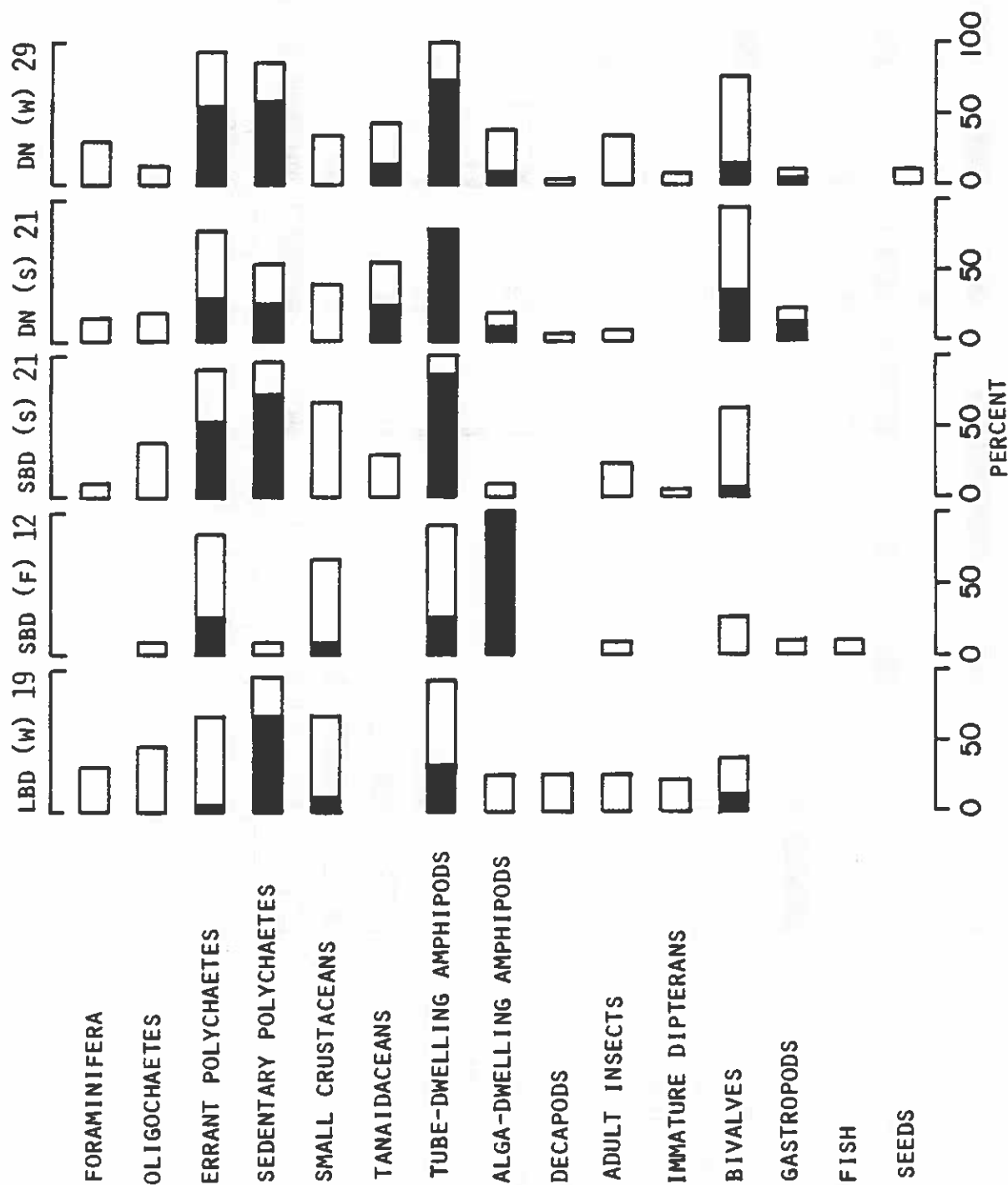


Figure 17. Percent of samples containing each prey type of the Long-billed Dowitcher (LBD), Short-billed Dowitcher (SBD) and Dunlin (DN). See Figure 8 for additional information.

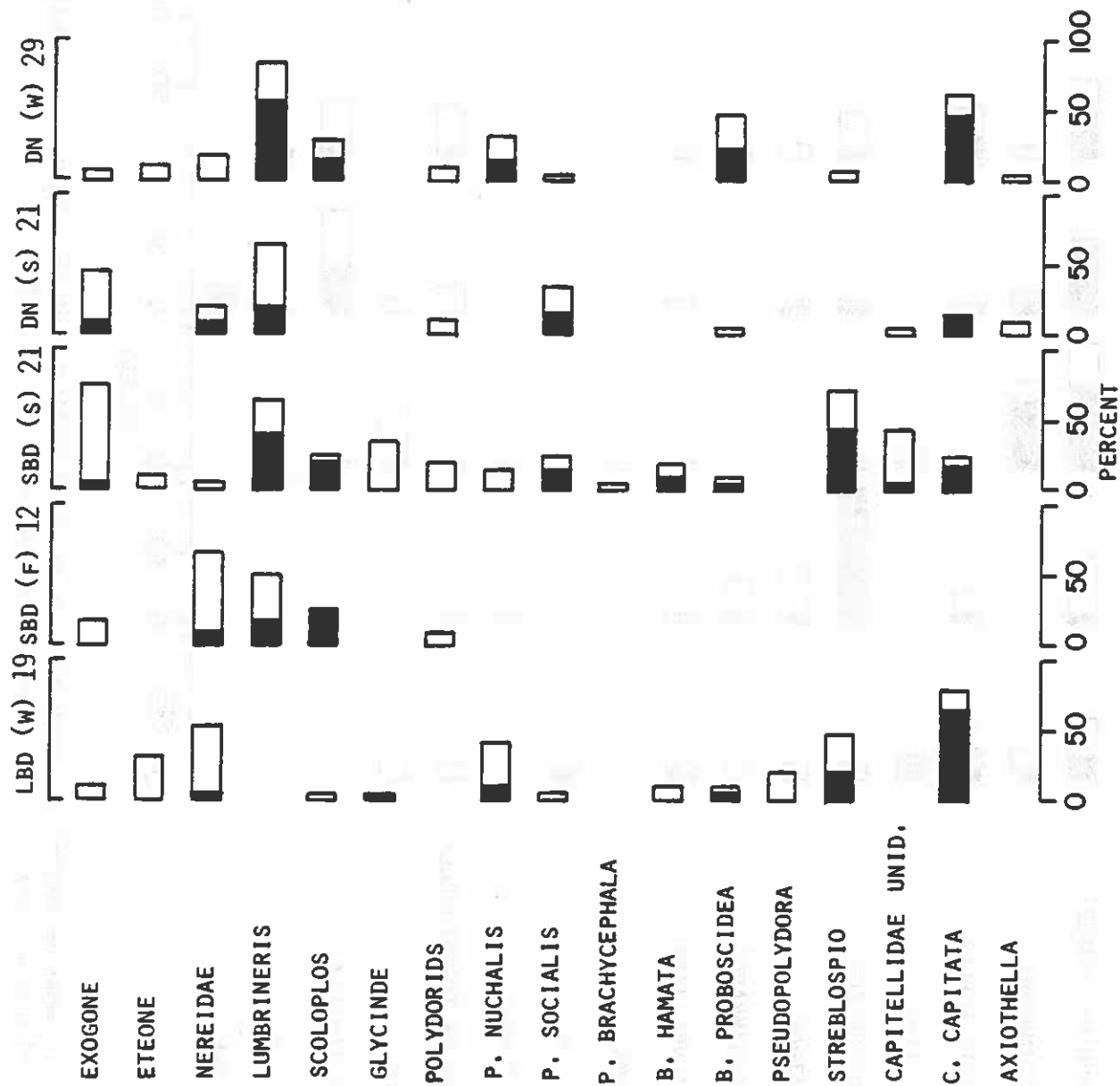


Figure 18. Percent of samples containing prey taxa of the Long-billed Dowitcher (LBD), Short-billed Dowitcher (SBD) and Dunlin (DN). See Figure 8 for additional information.

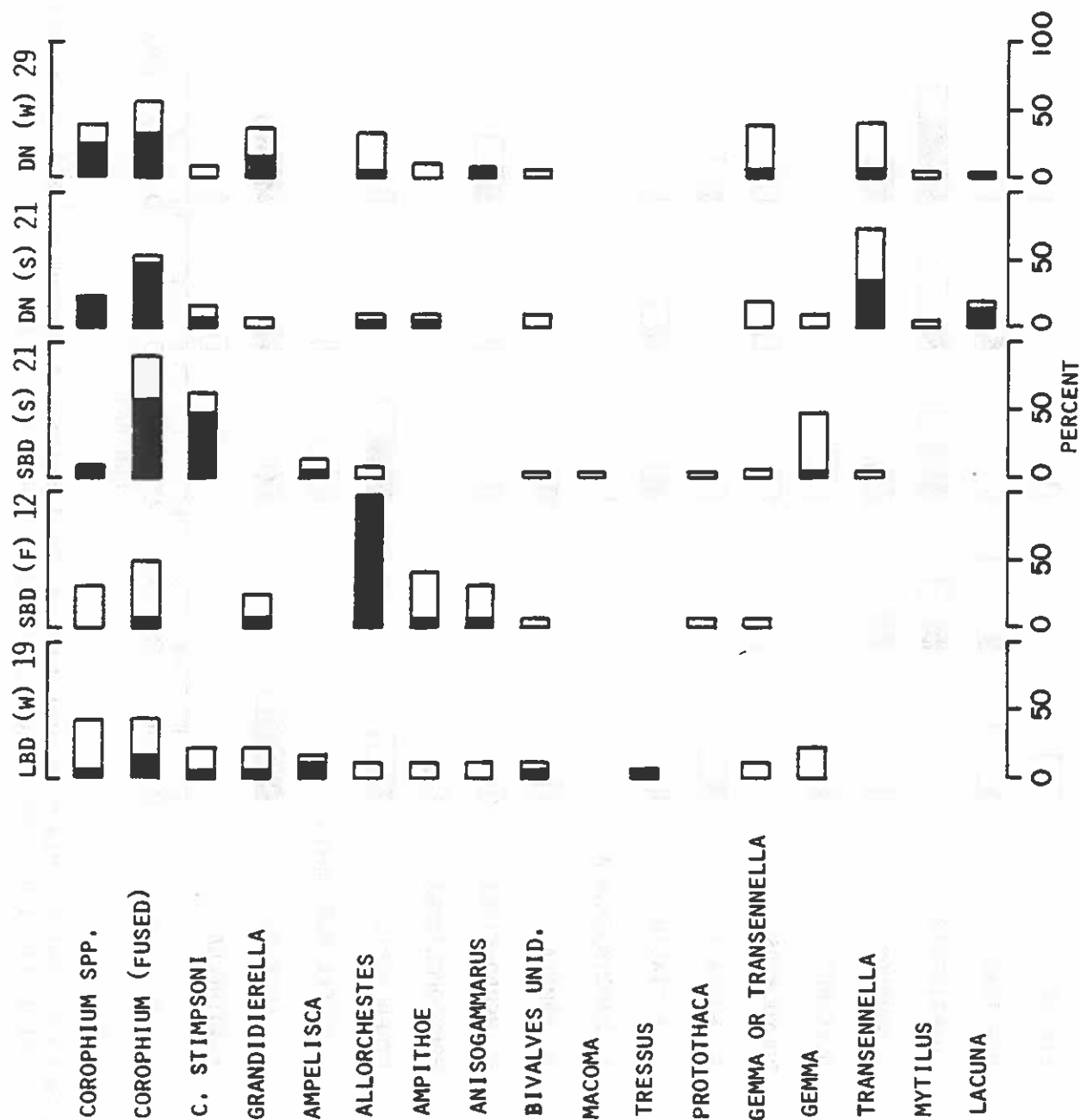


Figure 19. Percent of samples containing prey taxa of the Long-billed Dowitcher (LBD), Short-billed Dowitcher (SBD) and Dunlin (DN). For additional information see Figure 8.

Appendix 1. Diet of the Willet and Long-billed Curlew at Bolinas Lagoon.

FEEDING BEHAVIOR AND DIET OF THE LONG-BILLED CURLEW AND WILLET

LYNNE E. STENZEL, HARRIET R. HUBER, AND GARY W. PAGE

To study shorebird feeding ecology, most people collect birds and examine stomach contents although in a few instances regurgitated pellets (Hibbert-Ware and Ruttledge 1944, Swennen 1971) or observations of feeding birds (Baker and Baker 1973) have been used. In this study we used both observations and regurgitated pellets to examine the feeding behavior and the diet of the Long-billed Curlew (*Numenius americanus*) and the Willet (*Catoptrophorus semipalmatus*) on Bolinas Lagoon, in California. Our objective was to find a suitable method for studying shorebird diets without sacrificing the birds. In the literature we found little information on the diet of the Long-billed Curlew, and data on the Willet in California that we found are limited to the examination of 21 stomachs (Reeder 1951, Recher 1966, Anderson 1970). There is little information on the feeding behavior of either species. We felt, therefore, that any information we could add on the feeding behavior and diet of these shorebirds would be useful.

METHODS

Bolinas Lagoon is a shallow 570-ha estuary 24 km northwest of San Francisco, California. High hills, marshy pastures, and the Seadrift sand spit surround this wedge-shaped estuary except for a narrow opening to the ocean on the southwest side (Fig. 1). Pine Gulch Creek drains into the estuary year round and is the main source of the estuary's fresh water. Kent Island is a 40-ha island within the estuary. A large part of Kent Island and the Pine Gulch Creek delta are salt marsh where the chief plant species are *Salicornia virginica* and *Spartina foliosa*. At mean low water about 70% of the estuary comprises tidal flats which are divided by several channels (Ritter 1969).

This study was conducted from June 1973 to February 1974 and divided into a fall period (July through October) corresponding with a warm dry season, and a winter period (November through February) corresponding with most of the rainy season at Bolinas.

We made a census of all shorebirds on the estuary during every 5-day period from 31 May to 7 October and with one exception during every 10-day period from 8 October to 1 March. All but 2 censuses were taken on flood tides 1.1-1.7 m above mean low water. During the census the estuary was divided into 3 areas and an observer in each area counted or estimated all shorebirds in that area. The counts in the areas were made simultaneously.

Additional censuses of specific areas on or near the estuary were also made to find out which were most used by the birds. We censused shorebirds in the salt marsh on Kent Island at low and moderate tides several times a month, and on

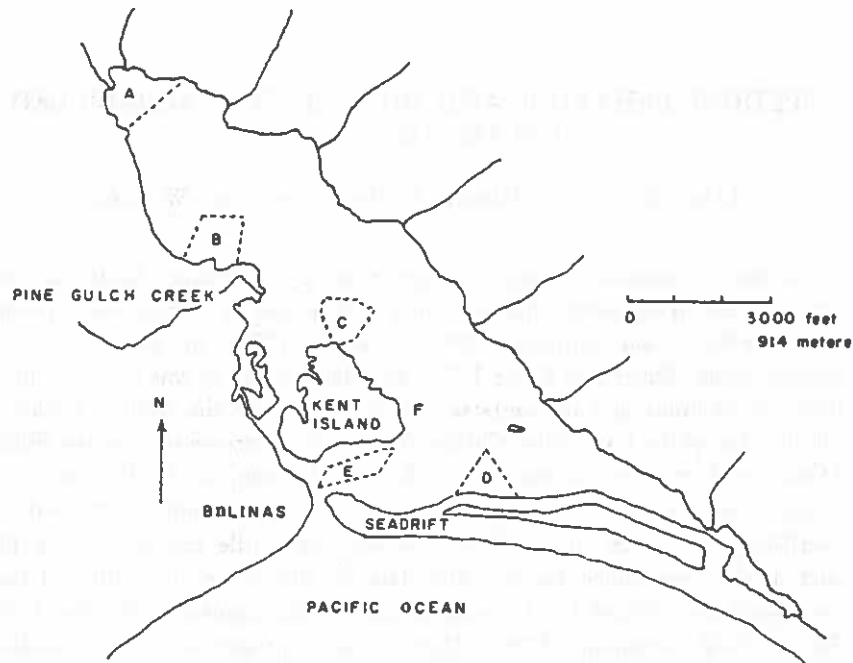


FIG. 1. Map of Bolinas Lagoon showing 5 areas of intensive study. Area A is approximately 12.6 ha; B, 9.8 ha; C, 8.0 ha; D, 7.0 ha; and E, 8.4 ha.

8.5 km of open coast (comprising sand to pebble beaches and soft shale reefs) adjacent to and north of Bolinas Lagoon 3 times a month.

We selected 5 areas within the tidal flat of the estuary (Fig. 1) for the most intensive study. The substrate of area A was a very poorly sorted, very fine sand (Ritter 1969) containing considerable organic debris such as twigs and leaves. Much of the high-water zone of this area was covered by a layer of sediment, dried and cracked into leathery plates. The high-water zone abutted a small salt marsh through which a fresh-water stream ran year round; the low-water zone bordered a basin. Area B was similar to area A except that a fresh-water stream ran into it only during periods of heavy rain and that the substrate ranged from fine to medium sand (Ritter 1969). The substrate of area C was a well to moderately sorted, fine sand (Ritter 1969) and lacked the organic debris of areas A and B. Unlike areas A and B the high-water zone of area C was pock-marked with the burrow openings of the ghost shrimp (*Callinassa californiensis*) and was not covered by hard, dried plates of sediment. The high-water zone of area C abutted the Kent Island salt marsh on one side and a channel on the other; the low-water zone bordered a small basin. Area D had a substrate of moderately sorted, fine sand (Ritter 1969), and was bordered on 2 sides by channels and on a third side by a basin. The high-water zone in the center was less burrowed than area C. Area E differed markedly from the other

areas. It comprised sediment ranging from medium sand through pebble. The pebble fraction contained numerous shell fragments and was largely in the low-water zone. The high-water zone was separated from the Kent Island sand beach by a shallow channel: the low-water zone bordered a main channel.

To find out where shorebirds fed on the tidal flat, 10 censuses, in which feeding and non-feeding birds were counted separately, were made in each of the 5 areas every month of the study. Each month we tried to census on all combinations of high, moderate, and low water with an ebb tide, a flood tide, and slack water. We tried to take censuses for a particular tidal condition in all areas on the same day.

We further divided each of the 5 areas into microhabitats, defined by elevation in the tidal zone and the water level in relation to the substrate surface. We defined the high-water zone of each area as the highest third of the area, the low-water zone as the lowest third, and the mid-water zone as the area between. In each zone, surface irregularities on the tidal flat such as pools and channels created emerged, edge (substrate holding a surface film of water), and submerged substrate, giving a total of 9 microhabitats. Recher (1966) and Baker and Baker (1973) also used the water level in relation to the substrate surface to describe tidal flat microhabitats. During the study, we censused at low tide in each area, counting the number of individuals of each species feeding in each of the microhabitats. Birds feeding in algae were counted separately.

Substrate cores were taken at low tide from each area to measure the relative abundance of small invertebrates, and from an invertebrate study plot to measure the seasonal abundance of some invertebrates. The cores, 9.8 cm deep and 6.6 cm in diameter, were washed through sieves with 1 mm openings and the organisms retained were identified and tallied. Nine cores were taken from each microhabitat (with the exception of a few very limited microhabitats) from all areas in June and from areas A, D, and E in December. The invertebrate study plot (280 × 20 m) lay along the southern border of area C and ran from the edge of the salt marsh to a basin in the low-water zone. Every month 2 cores were taken at random from each of 28 stations (10 × 20 m) along the length of the plot. Each month we estimated the algal coverage in each station.

As an estimate of the availability of the tidal flat to shorebirds, we calculated the number of daylight hours during which the tidal level was less than 1.4 m above mean low water. This calculation was made for one day of every 3-day period of the study; we used the tidal charts to estimate the rate at which the water ebbed or flooded and the time at which the water level reached 1.4 m above mean low water.

We watched individual Long-billed Curlews and Willets to determine their feeding rates, methods of searching for and capturing prey, use of microhabitats, and the type of prey they captured. We observed birds through 20× spotting scopes and tape-recorded data. The type, success, and microhabitat location of each prey-capture attempt were recorded as well as interactions between the bird under observation and other birds. Prey-capture attempts were defined as follows. A *peck* was a single movement of the bill usually to the surface of the mud but occasionally at flying insects or organisms on snags or rocks. A *multiple peck* was a series of 2 or more consecutive movements of the bill to the surface of the substrate without lifting the bill back to the horizontal position. *Probes* were single movements of the bill into and out of the substrate, that appeared to penetrate the substrate at least 1 cm. *Multiple probes* consisted of 2 or more vertical motions of the bill during which it was not withdrawn from the substrate. All pecks and probes were considered

prey-capture attempts although a few may have been search tactics. An observation was terminated when the bird stopped feeding and only observations of 4 min or longer were analyzed. Observations of Long-billed Curlews were taken at many locations on the estuary but those of Willets only in areas A, C, D, and E. In the fall period we made 46 Long-billed Curlew observations totaling 744 min and 28 Willet observations totaling 164 min; in the winter period, 22 Long-billed Curlew observations totaled 272 min and 67 Willet observations totaled 499.5 min. The average distance of the observer from the bird was 50 m for the Long-billed Curlew and 30 m for the Willet. In the Willet feeding observations, differences among areas are taken from winter observations only and differences between seasons from observations in areas A and C only because we did not collect an adequate sample of Willet observations in all areas for both seasons.

We analyzed regurgitated pellets of Long-billed Curlews and Willets to identify their prey. Most pellets were collected from locations where a group of roosting birds of a single species had just been flushed, but a few were collected from individuals after pellet regurgitation had been observed. Only moist, fresh pellets were collected; they were preserved in alcohol for later analysis. In the fall period 30 Long-billed Curlew pellets were collected on high tides in the salt marshes of the Pine Gulch Creek delta and Kent Island where most of the curlews on the estuary roosted. No curlew pellets were obtained during the winter period. Willet pellets were obtained from birds that fed in areas A, C, D, and E and roosted in the high-water zone of these areas during flood tides and from area F (Fig. 1) where many Willets that fed over a large portion of the estuary roosted. In the fall period we collected 19 Willet pellets from area A, 14 from C, 10 from D, and 15 from F; in the winter period, 2 from A, 7 from C, 4 from D, 2 from E, and 9 from F. We also obtained 6 stomachs from Willets that had been eaten by raptors and used 2 additional stomachs obtained in previous years from raptor kills. The contents of the pellets and stomach samples were examined under a 30 $\times$ dissecting microscope and the prey identified from characteristic fragments.

Two statistical procedures were used to test the similarity of one result against another: the test for the equality of 2 percentages (Sokal and Rohlf 1969:607-608) and Student's *t*-test for the difference between means (Steel and Torrie 1960:73-75).

In this paper mud crab is used synonymously with *Hemigrapsus oregonensis*, ghost shrimp with *Cullianassa californiensis*, and mud shrimp with *Upogebia pugettensis*.

RESULTS

Long-billed Curlew

Distribution.—During this study the number of Long-billed Curlews on Bolinas Lagoon consistently averaged 40. At nearby estuaries such as Limantour Estero, Tomales Bay, and Drake's Estero, 1 or 2 curlews were all that could be found on any date. On Bolinas Lagoon the curlews were scattered at low tide over the tidal flat, feeding primarily in emerged and submerged microhabitats; when the flats were covered at high tide the birds roosted in the salt marsh. Curlews were not seen feeding on the coast or in pastureland but occasionally one or two were seen feeding in the salt marsh.

TABLE 1
MEAN FEEDING RATES OF THE LONG-BILLED CURLEW FOR 2 FEEDING METHODS AND 2 SEASONS ON BOLINAS LAGOON

	Combined Seasons		Combined Methods	
	"Pause-probe"	"Burrow-probe"	Fall Period	Winter Period
PCA ^a /Min.	5.6	^{ab} 9.4	8.5	[*] 11.1
Prey/PCA (%)	8.5	[*] 4.9	4.9	4.8
Prey/Min.	0.4	0.4	0.3	[*] 0.5

^a PCA is prey-capture attempts.

^b An asterisk indicates a significant difference ($P < 0.05$) between adjacent means.

Feeding behavior.—Long-billed Curlews used 3 methods to obtain prey. In the "burrow-probe" method, used primarily in the emerged areas, the curlews probed into burrows until prey was sensed, then probed rapidly in a burrow until the prey was seized. In the "pause-probe" method, used only in submerged areas, the curlews stood in 5–10 cm of water with their bills partly under water and slightly ajar. They remained motionless in this position for 5–10 sec, presumably until detecting some movement in a burrow below. The bill was then moved slowly down until, with a sudden lurch, the prey was captured. If this attempt was unsuccessful the movement was often repeated. The burrow-probe and the pause-probe methods were used by the curlews to obtain all of their major prey species. The third capture technique, the "peck," was used much less often than the other methods and only to obtain prey on the substrate surface. The curlews were not observed to obtain any small prey by this method and only a few small, surface-dwelling prey were detected in the pellets. However, the curlews did obtain the mud crab with this technique. When a crab was sighted the curlew ran swiftly toward it. If the crab escaped to a burrow, the curlew often ignored the burrow entrance and probed directly through the mud to capture the crab. The curlews often switched among the 3 feeding methods.

Birds using the burrow-probe method made significantly ($P < .05$) more attempts per minute but were successful less often than birds using the pause-probe method (Table 1). There was no significant difference ($P > 0.05$) between the methods in the number of prey obtained per minute and no apparent difference in the size of the prey taken. In the winter period more attempts were made and more prey obtained per minute ($P < 0.05$) than in the fall (Table 1). However, the number of prey captured per attempt was nearly the same for both seasons ($P > 0.05$).

Appendix 1. (cont.).

Although many prey were eaten whole, prey that were particularly large or lively were not. The bird first removed some or all of the legs from such a prey by biting them off or by holding the prey by a leg and shaking it vigorously. The body was eaten first, then the legs. Claws of large male ghost shrimps were sometimes left uneaten. The curlews often washed muddy prey before eating them.

Willetts and Ring-billed Gulls (*Larus delawarensis*) sometimes attempted to steal prey from Long-billed Curlews. In 9 attempts during feeding observations Willetts were successful twice and in 10 attempts the Ring-billed Gulls successfully usurped a curlew's prey 3 times.

Diet of Long-billed Curlews.—Of the 30 pellets collected during the fall period 97% contained the remains of mud crabs, 77% of ghost shrimps, and 47% of mud shrimps. Of the 370 large invertebrates found in the pellets 59% were mud crabs, 34% ghost shrimps, 6% mud shrimps, and 1% unidentified decapods. In addition to the large prey, in the pellets were also remains from 9 insect pupae, 6 *Gemma gemma*, 3 seeds, 3 *Cryptomya californica*, 1 worm (Nereidae), and 1 *Littorina scutulata*. Fragments from several amphipods (Talitridae) were found in 2 pellets and traces of adult insects in 7 pellets.

From direct observations of 205 prey items observed being taken by curlews during the fall period, 55% were mud crabs, 24% ghost shrimps, 15% mud shrimps, and 7% were unidentified. During the winter period the direct observations on type of prey eaten were similar to those of the fall period: of 134 prey, 63% were mud crabs, 20% ghost shrimps, 7% mud shrimps, and 9% were unidentified. Occasionally during winter censuses on Bolinas Lagoon, but not during feeding observations, we saw Long-billed Curlews catch and eat small fish in submerged areas. No pellets were found during the winter period, perhaps because the curlews spent more time feeding and less time in the roosting areas than in the fall.

Willet

Distribution.—Willetts were the most abundant large shorebirds both on Bolinas Lagoon (averaging 560 birds during the fall and 385 in the winter period) and also on the adjacent coast (averaging 58 birds during the fall and 76 in the winter period). On Bolinas Lagoon, at low tide, most Willetts fed on the tidal flats; however, as the tide rose, the number of Willetts in the salt marsh increased until, at high tide, many Willetts were either feeding or roosting there. When high tides and rain coincided during the winter, flooding the intertidal areas, Willetts fed in the water-soaked pastures adjacent to the estuary. During all periods Willetts often flew

Appendix 1. (cont.).

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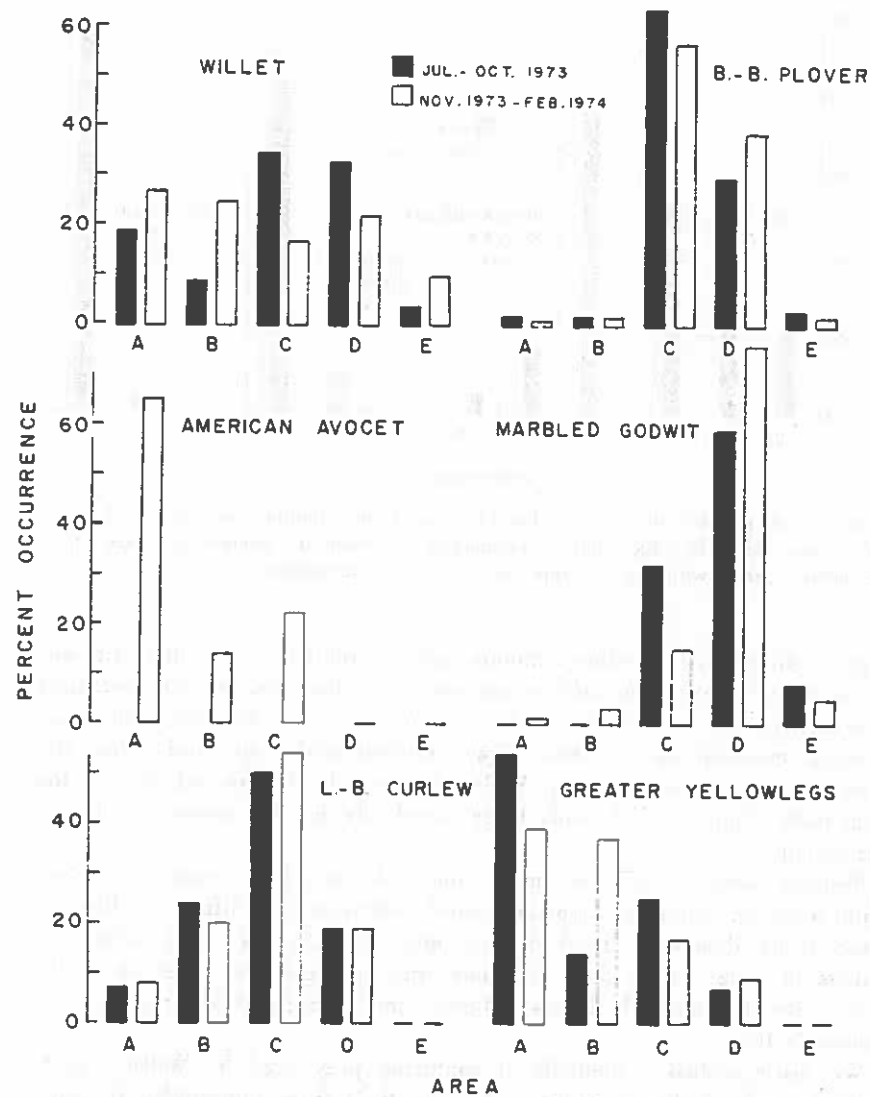


FIG. 2. Distribution of large shorebirds among 5 areas on Bolinas Lagoon. In the calculation of percent occurrence, equal weight was given to each month.

between the estuary and the adjacent coast indicating that both habitats were used by some of the birds.

Willetts fed over all of the tidal flat on Bolinas Lagoon and were more equally distributed among the different areas (Fig. 2) and microhabitats

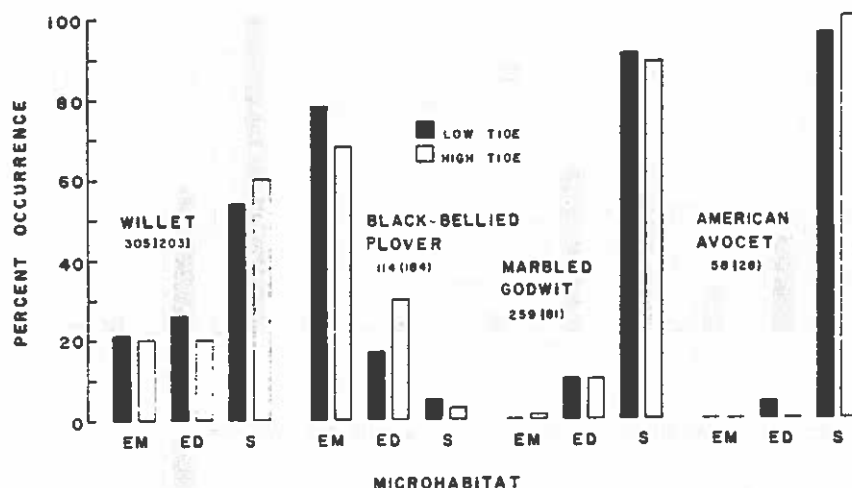


FIG. 3. Distribution of feeding shorebirds in 3 microhabitats on Bolinas Lagoon. EM is emerged; ED, edge; and S, submerged microhabitat. Sample sizes are under the species' names with the high-tide sample sizes in parentheses.

(Fig. 3) than were the other common large shorebirds: Long-billed Curlew, Black-bellied Plover (*Pluvialis squatarola*), American Avocet (*Recurvirostra americana*), Marbled Godwit (*Limosa fedoa*), and Greater Yellowlegs (*Tringa melanoleuca*). When algae, *Enteromorpha* sp. and *Ulva* sp., covered areas of the tidal flat, Willets fed heavily on invertebrates in the algal beds. They were the only large shorebirds that fed extensively in the salt marsh.

Feeding behavior.—Willets most commonly searched visually for prey while walking. Another important search technique was lifting or flipping algae, rocks, debris, or dried, cracked mud with the bill. Less commonly, Willets in water up to their tibio-tarsi ran erratically and pecked in the water. By this method Willets obtained small unidentified prey and occasionally fish.

We distinguished 5 methods of capturing prey used by Willets: peck, multiple peck, probe, multiple probe, and theft from Long-billed Curlews. In all areas studied Willets captured 93% or more of their prey with pecks and multiple pecks.

Capture of small prey was detected indirectly by movements of the head and swallowing motions but capture of large prey was easily seen and large organisms were often identified. Large prey such as fish or pelecypods were swallowed whole; decapods were often shaken apart, the

Appendix 1. (cont.).

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appendages then being eaten before the carapace. When large organisms were covered with mud, Willets often washed them before eating them. We saw Willets reject some prey: a few large cockles and crabs that the birds first struggled to swallow and then rejected (probably because they were too large) and large snails which the birds merely investigated. Willets sometimes lost large quarry to Ring-billed Gulls and Western Gulls (*Larus occidentalis*).

Diet of the Willets.—Pellets from Willets contained small organisms from the tidal flats such as the surface-dwelling gastropod *Cerithidea californica*, the pelecypods *Gemma gemma* and *Transenella tantilla*, and tube-dwelling amphipods (*Corophium* spp.). The amphipods *Allorchestes angustus* and *Ampithoe* spp., the gastropod *Lacuna* sp., and most of the mussels (*Mytilus* sp.) were taken from algae. The gastropod *Littorina scutulata* and some of the mussels (*Mytilus* sp.) found in the pellets were probably taken from tires, rocks, and snags; adult insects (mostly Coleoptera and Diptera) and talitrid amphipods (mostly or entirely *Orchestia traskiana*) were probably taken in the salt marsh. Remains of large prey in the pellets included the pelecypods *Protothaca staminea* and *Macoma* spp., the brachyurans *Hemigrapsus oregonensis* and *Cancer antennarius*, and the anomurans *Callinassa californiensis*, *Upogebia pugettensis*, and *Pagurus* sp. Other prey, occurring infrequently in the pellets, included the polychaetes *Capitella capitata*, *Lumbrineris zonata*, and an unidentified nereid, ostracods, the cheliferan *Leptochelia dubia*, the amphipod *Grandidierella japonica*, the brachyurans *Pachygrapsus crassipes*, *Hemigrapsus nudus*, and *Cancer magister*, larval and pupal dipterans, and the pelecypod *Clinocardium nuttallii*.

We detected additional tidal flat prey from feeding observations. While Willets took only one fish in 164 min of observation in the fall period, they captured 11 during 499.5 min of winter observation, mostly from areas D and E. During the winter period some Willets, feeding in the mid- and high-water zones of area A during rising tides, captured up to 19.7 worms per minute. Since several species of Spionidae constituted 85% of the worms in our samples from area A during the winter period, 1 or more of these were probably the worms that the Willets ate.

Cooper's Hawks (*Accipiter cooperii*), Red-shouldered Hawks (*Buteo lineatus*), and Marsh Hawks (*Circus cyaneus*) often hunted Willets in the salt marsh and sometimes left the entrails and flight feathers of Willets they had eaten there or under the pines on Kent Island. In the 8 stomachs left with such remains we found *Orchestia traskiana* in all, adult Coleoptera in 6, unidentified seeds in 6, *Littorina scutulata* in 4, the small gastropod

TABLE 2
MEAN FEEDING RATES OF THE WILLET DURING WINTER IN 4 AREAS ON
BOLINAS LAGOON

Area	PCA ^a /Min.	Prey/PCA (%)	Prey/Min.	% Large Prey ^b	Sample Size ^c
A	30.0	39.2	13.1	2.0	12
C	27.3	31.7 **	9.1 *	2.5	14
D	26.3	16.4 *	3.8 *	4.3 *	26
E	23.1	8.2	1.8	20.1	15

^a PCA is prey-capture attempts.

^b Large prey includes decapods, pelecypods greater than 3 cm long, and fish.

^c Sample size is the number of feeding observations used to calculate the means.

^d An asterisk indicates a significant difference ($P < 0.05$) between adjacent means.

Phytia setifer in 3, *Lacuna* sp. in 2, *Hemigrapsus oregonensis* in 2, *Gemma gemma* in 1, and *Mytilus* sp. in 1.

Inter-area variation.—The Willets' feeding success varied among different areas of the tidal flat. Although the number of prey-capture attempts per minute did not differ significantly between any of the areas (for all possible pairs of data, $P > 0.05$), the success rate (prey per prey-capture attempt) differed significantly ($P < 0.05$) between some areas and resulted in different rates of prey intake between areas (Table 2). A trend for the number of prey per minute to decrease from areas A to E may have been partially offset by a tendency for large prey to make up an increasing percentage of the diet from areas A to E (Table 2). Among areas there was also considerable variation among the microhabitats in which Willets fed (Table 3).

As expected, variations among different areas in the abundance of the

TABLE 3
USE OF DIFFERENT MICROHABITATS BY WILLETS DURING WINTER IN 4 AREAS
ON BOLINAS LAGOON

Area	Percent of PCA ^a			Sample Size	Percent of Prey Taken			Sample Size
	Em ^b	Ed	S		Em	Ed	S	
A	0.2	55.9	43.9	2273	0.1	68.0	31.9	1025
C	1.0	5.8	93.1	2477	1.6	4.2	94.2	738
D	8.8	15.2	76.0	4731	12.1	19.4	68.5	660
E	38.0	2.9	59.1	2141	49.7	2.5	47.8	157

^a PCA is prey-capture attempts.

^b Em is emerged, Ed is edge, and S is submerged.

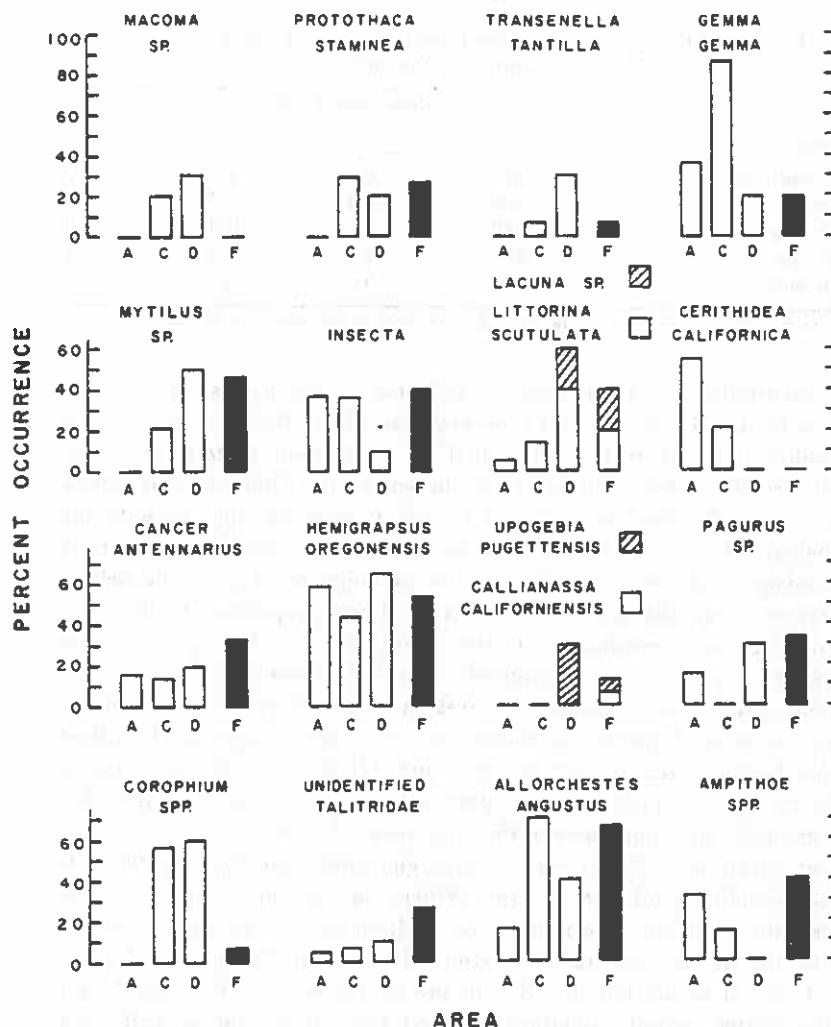


FIG. 4. Percent occurrence of prey in Willet pellets collected from 4 areas of Bolinas Lagoon from July to October 1973. Pellets collected in areas A, C, and D were from birds feeding in or in the vicinity of those areas; pellets from area F were from birds feeding over a large area of the estuary. Sample size for A is 19; C, 14; D, 10; F, 15. Two additional pellets from area E contained a total of 4 *Pagurus* sp., 5 *Pachygrapsus crassipes*, and 3 *Hemigrapsus oregonensis*.

TABLE 4
RELATIVE ABUNDANCE OF SELECTED INVERTEBRATES IN 4 AREAS ON
BOLINAS LAGOON IN JUNE 1973

Species	Mean Number per Core in Area ^a			
	A	C	D	E
<i>Cerithidea californica</i>	0.1	0.1	0.0	0.0
<i>Gemma gemma</i>	152.6	28.0	4.6	0.0
<i>Transenella tantilla</i>	0.0	0.1	12.1	0.0
<i>Corophium</i> spp.	21.7	41.0	56.9	45.4
Number of cores	9	9	9	9

^a Means are from microhabitats with the highest abundance of the organism in each area.

tidal flat invertebrates were sometimes reflected in the pellets. There was an increase in the abundance of *Transenella tantilla* in the substrate (Table 4) and pellets (Fig. 4) from area A to C to D. *Gemma gemma* and *Cerithidea californica* were less abundant in the substrate (Table 4) and pellets (Fig. 4) of area D than areas A and C, and *Corophium* spp. were found only in pellets (Fig. 4) from the areas in which these amphipods occurred most abundantly (Table 4). The relative abundance of prey in pellets from different areas did not always occur in direct proportion to the relative abundance of invertebrates in the substrate. For example, *Gemma gemma*, which occurred most frequently in pellets from area C, occurred most abundantly in the substrate of area A. The abundance of prey in each area, such as *Littorina scutulata* on rocks and snags or *Ampithoe* spp., *Allorchestes angustus*, *Lacuna* sp., and *Mytilus* sp. which occurred primarily on algae, depended on properties that we did not measure. We did not sample for the abundance of the large invertebrates.

Seasonal variation.—There were several environmental changes that affected the availability of prey to the Willets on the tidal flats from the fall to the winter period. The number of daylight hours that were available for feeding on all but the highest portion of the tidal flat decreased from a mean of 10.1 h in the fall to 7.3 h in the winter period. Prolonged rain during the winter period sometimes flooded the estuary for several days and further reduced the number of daylight hours that the tidal flats were available.

There was a decrease in the abundance of some of the Willets' prey from the fall to the winter period. Numbers of substrate-dwelling invertebrates *Gemma gemma* and *Corophium* spp. and alga-dwelling invertebrates *Allorchestes angustus* and *Ampithoe* spp. all declined from the fall to the winter period (Table 5). The decline in alga-dwelling amphipods was probably

TABLE 5
SEASONAL ABUNDANCE OF SOME OF THE WILLETS' PREY ON BOLINAS LAGOON

Species	Location ^a	Mean Number per Core in:	
		Fall Period	Winter Period
<i>Gemma gemma</i>	Area A	152.6	14.7
	I.S.P.	4.9	2.3
<i>Corophium</i> spp.	I.S.P.	20.1	4.0
	Area D	56.9	10.6
<i>Transenella tantilla</i>	Area D	12.1	4.9
<i>Allorchestes angustus</i>	I.S.P.	6.1	0.1
<i>Ampithoe</i> spp.	I.S.P.	0.2	0.0

^a Data from areas A and D taken from 9 cores from the microhabitat in each area in which each organism occurred most abundantly. Data from the invertebrate study plot (I.S.P.) taken from 56 cores per month during each period.

^b An asterisk indicates a significant difference ($P < 0.05$) between fall and winter period means.

related to a decline in the extent of the algal beds on the estuary. In July algae (primarily *Enteromorpha* sp.) covered 57% of the invertebrate study plot, in August 41%, in September 20%, in October 3%; from November to February only an insignificant area was covered. *Ulva* sp., another green alga, covered 2.1% of the invertebrate study plot in the fall period and only 0.4% in the winter.

The success of Willets' feeding attempts (prey per prey-capture attempt) decreased ($P < 0.05$) from 70.7% in 22 fall observations to 35.2% in 26 winter observations. In censuses of birds in the different areas the proportion of Willets feeding at any time increased ($P < 0.05$) from a mean of 84.0% of the total birds censused in fall to 92.1% in winter. This was probably due to increased pressure on the birds to use more of the available feeding time in the winter than in the fall period. There were also seasonal changes in the Willets' use of different feeding areas within and near the estuary. During fall 26.1% of 890 Willets censused in areas A, B, C, and D were feeding in algae but during the winter period only 6.7% of 378 birds were feeding in the much depleted algal beds. The number of Willets feeding in the Kent Island salt marsh at low and moderate tides increased ($P < 0.05$) from 5.0% of the estuary's Willets in fall to 17.5% in winter. The number of Willets found on the open coast also increased ($P < 0.05$) from 9.2% of the combined estuary and open coast Willet population in the fall to 17.3% in the winter period. It appears that the decreased availability of the tidal flat and the decline in abundance of some tidal flat invertebrates resulted in increased daytime use of feeding areas other than the tidal flat from the fall to winter period for the Willets. We found Willets feeding

TABLE 6
SEASONAL DIFFERENCES IN WILLETS' PREY FROM PELLETS^a COLLECTED FROM
AREAS C AND F ON BOLINAS LAGOON

Prey of Willet	% of Pellets in which Prey Occurred	
	Fall Period	Winter Period
<i>Pagurus</i> sp.	17	0
<i>Gemma gemma</i>	52	12
<i>Corophium</i> spp.	31	0
<i>Ampithoe</i> spp.	28	0
<i>Allorchestes angustus</i>	69	6
<i>Mytilus</i> sp.	34	6
<i>Cancer antennarius</i>	24	6
<i>Lacuna</i> sp.	10	12
<i>Cerithidea californica</i>	10	12
<i>Littorina scutulata</i>	17	19
<i>Macoma</i> spp.	10	12
<i>Protothaca staminea</i>	28	38
<i>Transenella tantilla</i>	7	12
<i>Callinassa californiensis</i>	3	12
<i>Upogebia pugettensis</i>	3	19
<i>Hemigrapsus oregonensis</i>	48	94
adult Insecta	38	69
Talitridae ^b	17	50
sample size	29	16

^a Significant seasonal differences ($P < 0.05$, test for equality of 2 percentages) are indicated by an asterisk.

^b Talitridae are mostly or entirely *Orchestia trossiana*.

on the tidal flats at night during the winter, but during the fall our observations suggest that most Willets leave the estuary at or shortly after dusk. There may be a greater tendency for Willets to feed at night during the winter than during the fall period.

A change in the diet from the fall to the winter period was detected in the pellets (Table 6). *Allorchestes angustus*, *Ampithoe* spp., and *Corophium* spp. were major prey in the fall but nearly absent from the winter pellets. The presence of *Gemma gemma* in the pellets decreased from the fall to the winter period. As already described, our substrate samples also showed a decline in these species during winter (Table 5). *Mytilus* sp. and *Pagurus* sp. decreased from the fall to the winter period in the pellets but we have no information on their seasonal abundance. The increase during the winter period of some amphipods (Talitridae) and insects (mostly Coleoptera) in the pellets is probably a reflection of the increased use of the salt marsh by the Willets during this period.

DISCUSSION

On Bolinas Lagoon the Long-billed Curlew is a hunter of large burrow-dwelling prey and its exotic morphological features are in harmony with this pursuit. Its major prey species live in different habitats but all have curved burrows. Mud shrimps live at low tide levels in U-shaped burrows that extend about 45 cm into the substrate (MacGinitie and MacGinitie 1968). Ghost shrimps live in a higher tidal zone than mud shrimps, in many-branched burrows that extend vertically into the substrate (MacGinitie 1934). Both organisms feed near the entrance of their burrows. Mud crabs live throughout most of the estuary in horizontal burrows or under algae and debris. The curlew is well adapted to obtain these prey as the length of its bill (average 16.5 cm, Dawson 1923) allows it to probe deeply into the substrate and the bill's curve fits nicely into the burrows. Curlews often twist their heads as much as 180°, apparently to follow the curve of a burrow with their bills.

The diet of the Long-billed Curlew on Bolinas Lagoon is not representative of the species in California since in California Long-billed Curlews are more abundant inland than along the coast (Jurek 1973). Curlews that live inland must rely on terrestrial and fresh-water organisms for their food. Such a diet is indicated from the limited information in the literature which gives insects of several families, spiders, berries, crayfish, snails, fiddler crabs, amphipods, and occasionally nestling birds as food of the Long-billed Curlew (Wickersham 1902, McLean 1928, Sugden 1933, Palmer 1967, Timken 1969). Comprehensive studies of curlews feeding in various inland habitats are necessary for a more representative picture of this bird's diet in California.

In contrast to the curlew, the Willet occurs primarily along the coast when not on the breeding grounds (Jurek 1973). At Bolinas Lagoon the Willet was much more opportunistic in obtaining prey than was the Long-billed Curlew. Willet pellets contained at least 30 different prey from a wide variety of habitats but curlew pellets contained primarily 3 burrow-dwelling decapods and only small numbers of other invertebrates. Seasonal changes in the diet were prominent for the Willet but not the Long-billed Curlew. Other people studying shorebirds along the California coast found the Willet eating different organisms than at Bolinas Lagoon. Reeder (1951) found *Hemigrapsus oregonensis* present in 2 and cirratulid worms present in 1 of 2 Willet stomachs collected in May from Orange Co. Recher (1966) collected 16 Willets at one location on San Francisco Bay from September through May and found in decreasing order of abundance in the stomachs *Gemma gemma*, *Ilyanassa obsoleta*, *Nereis succinea*, *Mya arenaria*, *Macoma inconspicua*, *Hemigrapsus oregonensis*, and

TABLE 7
PREY OF WILLETS COLLECTED IN THE SAN FRANCISCO BAY AREA

	Number of Stomachs in which Each Prey Occurred		
	San Francisco Bay		
	San Pablo Bay ^a	Bay Tidal Flats ^a	Leslie Salt Ponds ^b
Annelida	1	6	
Decapoda	1	1	
Isopoda		1	
<i>Ephydra cinerea</i> larva			3
<i>Ephydra cinerea</i> pupa			1
Ephydriidae larva		2	
Ephydriidae pupa		2	
Ephydriidae adult		1	
Corixidae		1	
Insecta		1	
Arachnida	1		
<i>Macoma inconspicua</i>	5	3	
<i>Protothaca semidecussata</i>		1	
<i>Gemma gemma</i>		4	
<i>Mytilus</i> sp.		6	
Pelecypoda		2	1
<i>Hyunassa obsoleta</i>	3	4	
Gastropoda		4	2
<i>Cottus</i> sp.		4	
Pisces	1		
empty stomachs	3	1	
total number of stomachs	9	11	3

^a Unpublished data from California Department of Fish and Game.

^b Data from Anderson 1970.

Voltsella demissa. Additional information on the diet of the Willet, collected by the California Department of Fish and Game, is summarized in Table 7. Because the Willet's diet is so varied it is apparent that studies from many coastal habitats are necessary before a representative diet for the Willet on the California coast will be adequately documented.

If we had obtained stomachs instead of pellets in this study it would have been equivalent to removing 75% of the Long-billed Curlews and 21% of the Willets on Bolinas Lagoon during the winter period. Consequently, we needed an alternative to collecting the birds in order to study their diet and an important consideration of the study was to determine the usefulness of feeding observations and pellets to meet this end. The Long-billed Curlews' 3 major prey were easily identified in feeding obser-

vations because of their large size and in pellets because of their digestion-resistant claws. The relative frequency with which the 3 prey species were taken by Long-billed Curlews on Bolinas Lagoon could not be measured from feeding observations because the observations were not taken with regard to the distribution of the curlews on the estuary, or from pellets because pellets were collected at high tide and consequently emphasized the prey taken on a rising tide. Most of the Willets' prey were too small to be identified in feeding observations and too broken down in the pellets for us to tally the number of individuals making up the remains. Swanson and Bartonek (1970) for waterfowl and Tuck (1972) for shorebirds reported that wide variation occurs in the digestibility rates of different prey. Considerable variation in the digestibility rates of the Willets' many prey certainly must have occurred and further hindered interpretation of the results. Hartley (1948) has discussed in detail the problems in analyzing stomach contents posed by variation in digestibility rates of different prey. Many of the problems are similar for the analysis of stomach contents and pellets, but our lack of knowledge of the factors causing pellet regurgitation in shorebirds and our inability to collect pellets under all tidal conditions are specific problems related to pellets. Because the shortcomings of analyzing stomach contents and pellets are similar in many ways, we feel that shorebird pellets and stomach contents in many instances can provide comparable information on the birds' diet. Observations of feeding birds can be very useful in extending the information on diet drawn from the examination of pellets or stomach contents.

SUMMARY

Visual observations and regurgitated pellets were used to study the feeding behavior and the diet of the Long-billed Curlew and Willet on Bolinas Lagoon from July 1973 through February 1974. Samples of the invertebrates in the tidal flats were collected at different locations and at different times to obtain information on their spatial and temporal distribution for comparison with the shorebirds' diets. The Long-billed Curlews' major prey were 3 large, burrow-dwelling decapods that the curlews obtained primarily by probing into burrows. No seasonal change was detected in the curlews' diet. Most of the Willets' prey were too small to identify in visual observations and too finely divided in the pellets to permit determination of the number of individual prey in each pellet. Therefore, the percentage of the pellets in which each prey occurred was used to compare the abundance of each prey species in the Willets' diet. The Willets' feeding behavior and diet were much more variable than the curlews'. The Willets' diet and feeding success varied among different areas in the estuary and between a fall and winter period.

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