THE FUNCTIONING OF BALLONA WETLAND IN RELATION TO TIDAL FLUSHING

PART I -- BEFORE TIDAL RESTORATION

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ABSTRACT

To test hypotheses about the functioning of estuaries, we collected detailed information about the soils, plants and animals at six channel sites and fifteen "marsh" sites in Ballona Wetland, from March to November 1990. Our results were:

THE CHANNEL SITES

1. Tidal range inside Ballona Wetland was greatly reduced. It was at most lm relative to a potential 2.7m , i.e, a 63% reduction in tidal amplitude.
2. Water salinity declined progressively upstream. A major freshwater inflow event dropped average water salinities from 35ppt in July to 5ppt in October.
3. Macroalgae were abundant and appeared to smother the benthos. Channel bottoms were anaerobic within 2mm of the sediment surface.
4. Benthic invertebrates were rare and declined upstream in relation to the salinity gradient and a 62% decline in abundance occurred following the freshwater intrusion in late summer.
5. The fish community was similar to the communities found in channels of tidal salt marshes but was lower in species richness and abundance . The abundance of mosquito fish throughout the system in October reflected the brackish water salinities.
6. Few birds used the channels.

THE "MARSH" SITES

7. The moisture content of the soil was highest in the western-most sites and declined towards the east. Soils in the salt marshes were low in moisture content and brackish, rather than waterlogged and hypersaline as in fully tidal salt marshes. The salt panne substrate was hypersaline all year. The old agricultural field soils were relatively dry and mildly saline.
8. Edaphic algal mats were lacking in all but the wettest marsh site.
9. Nitrogen content was relatively high in the marsh soils and probably did not limit vascular plant growth.
10. The salt marsh sites were dominated by *Salicornia virginica*, pickleweed. Pickleweed standing crops were much higher than in fully tidal systems, such as Mugu Lagoon and Tijuana Estuary. We believe that the pickleweed at Ballona Wetland had a somewhat higher productivity and a somewhat longer turnover time than at Mugu Lagoon.
11. Canopy heights of pickleweed appeared to reach a threshold at 55cm and were generally taller than in tidal estuaries. Although the plants growing in the old fields tended to grow taller, they had less biomass per m^2.

12. Pickleweed foliar nitrogen was high, 2-3 times higher than that at Tijuana Estuary.

13. Detritus production and decomposition rates were low relative to fully tidal marshes, with moisture being a likely limiting factor.

14. The marsh invertebrate community was dominated by amphipods, spiders and insects. Their numbers were higher in the wetter pickleweed sites than in the drier pickleweed sites.

15. Bird use of the "marsh" sites was minimal. Although Savannah Sparrows occurred in all habitats, males set up breeding territories in one area only. We hypothesize that they chose this area because it was isolated from human disturbance.

16. Red foxes bred in the wetland. As many as eight were seen in one day.

We conclude that Ballona Wetland is a remnant salt marsh that receives little tidal flow. In its channels, macroalgae can be abundant but animals are relatively rare. In its salt marshes, only pickleweed is abundant, soils are relatively dry, and animals are relatively rare. Although several exotic species (e.g., several plants, a snail, a fish, a mammal) have invaded the wetland, it does support many native species, and a small number of rare and sensitive species (e.g., the Savannah Sparrow). We expect that the restoration of tidal flow to Ballona Wetland will greatly improve conditions for the native species, reduce the populations of the exotic species, and improve the general functioning of the wetland.

INTRODUCTION

Restoration projects provide unique opportunities to ecologists -- they allow one to test one's understanding of a system in a large scale experiment (Diamond 1987). In fact Bradshaw (1987) argues that there is no more direct test of our understanding of the functioning of an ecosystem than to attempt to restore it to a fully functional ecosystem.

Ballona Wetland is a relatively small, remnant salt marsh that is the last major coastal marsh in Los Angeles County. Maguire Thomas Partners, the principal owners of Ballona Wetland, wish to restore the wetland by improving the opening to the ocean and reintroducing tidal flushing. PERL is conducting studies of the Ballona Wetland ecosystem in order to improve the restoration project, to allow assessment of the success of restoration project, and to test ideas about the functioning of southern California's coastal wetlands.

We have focused our research on the Ballona Wetland food web. The food webs of the southern California coastal wetlands have been relatively poorly studied. This is in contrast to the food webs of coastal systems elsewhere, e.g. Darnell (1961), Teal (1962), Day *et al.* (1973), Odum and Heald (1975), Wiegert et al. (1981). Studies of California coastal marshes have emphasized plant community composition (Hinde 1954, Vogl 1966, Zedler 1977) and changes in community structure following disturbances (e.g., Resh and Balling 1983, Zedler and Nordby 1986, Onuf 1987). Likewise, the research on California mudflats and channels has focused on community structure (e.g., Peterson 1977, Hosmer 1977, Homziak 1977, Allen 1980, Schreiber 1981, Seapy 1981, Nordby 1982, Onuf and Quammen 1983, Boland 1988, Nordby and Zedler in press).

Little is known about the factors that control the nature of the food web in an estuary as a whole. We hypothesize that physical factors play important roles. In particular, we hypothesize that water salinity and current speeds are important in channels, and soil moisture and soil salinity are important in marshes. It is these physical factors that will be altered by restoration of tidal flow to Ballona Wetland, thus providing a unique opportunity to test our hypotheses.

Our pilot study of Ballona Wetland (PERL 1989) included initial surveys of the dune, channel and salt marsh communities. However, we documented limited tidal flow in the salt marsh and noted various ecosystem attributes that appeared to relate to the reductions in tidal amplitude, tidal circulation, and water and soil salinities. For example, we noted the presence of extensive floating macroalgal mats in the channels. These algae appear to smother the benthos, create anoxic conditions in the channel sediments, and reduce the abundances of infaunal invertebrates (e.g., clams, polychaetes, ghost shrimps). Also, in the salt marsh we found the soils to be relatively dry, and epibenthos (both algae and animals) to be lacking. The vascular plants appeared to be relatively low in plant food quality and plant decomposition rates seemed low. Finally, the conditions of reduced tidal flow and reduced water and soil salinity appeared responsible for the invasion of several exotic species to both the channels and marshes.

Because of a greatly dampened tidal range within Ballona Wetland, we hypothesized that the marsh and channel habitats are relatively segregated. The small tidal flow can not provide the normal linkage between the two habitats. Aquatic organisms are largely restricted to the channels, and terrestrial organisms are restricted to the salt marsh and old fields. The current food web at Ballona Wetlands is no doubt complicated, but our pilot study (PERL 1989), suggested two major chains within the web: (a) the mainly terrestrial or salt marsh food chain that involves living vascular plants, insects and birds;

and (b) the mainly aquatic or channel food chain that involves algae, marine invertebrates and fish (Figure 1A). Birds from the marsh feed along the channel edges, providing at least one link between these two chains. However, links in the reverse direction appear limited. Marsh plant productivity has few opportunities to move into the channels, and channel consumers can not move into the marsh.

We predict that the restoration of tidal action to Ballona Wetland will have many impacts on environmental conditions and on the food chains (Figure 2). These impacts will be brought about by the increases in the current speeds in the channels, increases in the marsh soil moisture content, and increases in the salinity of the marsh soils and channel water. For instance, we predict that more birds will visit the restored wetland. This is because the increased current speeds in the channels will cause the macroalgal abundance to decline and the microalgae to increase, and these in turn will allow the number of benthic invertebrates to increase; these invertebrates are eaten by many species of sandpipers, plovers and gulls, but the invertebrates are also eaten by fish, which in turn are eaten by terns, herons, egrets, etc. We therefore expect more sandpipers, plovers, gulls, terns, herons, and egrets to be present in the restored Ballona Wetland.

A graphic representation of the hypothesized food web after tidal restoration (Figure 1B) incorporates these changes. In general, we hypothesize that these shifts will increase the linkages between the marsh and channel food chains and increase the variety and population sizes of most compartment. It is the predictions in Figure 2 that we proposed to test by this before-and-after study. When completed, i.e., when both the before-restoration and after-restoration data have been collected, our study will advance the knowledge of how southern California wetlands function, show how the food web changes in the areas that currently support wetland species, and identify the habitats that become functional wetlands.

In order to test the predictions we have set up 21 permanent study sites in the wetland and collected detailed information about the water, soils, plants and animals at each site. We plan to revisit these sites after restoration to measure the same factors and test our hypotheses. All sites have been clearly staked and labelled, all methods are fully described below so that they can be easily duplicated, and all the before-restoration results are presented in detail. We have not intended to inventory all the plants and animals that use the wetland. Instead we have focused on the lowland areas of the wetland, i.e., the areas most likely to be affected by the restoration of tidal flow, and have described the current conditions at these sites to allow quantitative assessment of the changes that are due to the restoration.

The research reported here is the first half of the complete study - i.e., the before-restoration condition at Ballona Wetland. We proposed to conduct research on the current functioning of Ballona Wetland for a full year, i.e., from February 1990 through February 1991, but we were funded for only three seasons of field work. Therefore in this report we present the results from our Spring, Summer and Fall 1990 field work.

Finally, of vital concern to the restoration of Ballona Wetland is the presence of a small population of Belding's Savannah Sparrows. The Belding's Savannah Sparrow (*Passerculus sandwichensis beldingi*) is the only endangered bird species that currently breeds and winters in the Ballona Wetland. It has been the focus of another research project by Barbara Massey and Ken Corey. Last year they found between nine and 31 breeding territories in the wetland (PERL 1989). They have continued to monitor the distributions, abundances and breeding activities of the Belding's Savannah Sparrow in Ballona Wetland (Corey and Massey 1990) and we draw on some of their 1990 results in our discussion.

METHODS

Seven habitats were identified in the Ballona Wetland: proximal and distal channels; eastern, central and western *Salicornia virginica* marshes; salt pannes; and old agricultural fields. Three sampling sites were chosen for intensive study in each of the habitats, making a total of 21 sites: 6 channel sites and 15 "marsh" sites (Figure 3).

We have defined the seasons as Spring (March, April and May), Summer (June, July and August), and Fall (September, October and November). Some data were collected every month (e.g., bird numbers), but most were collected once per season during the middle month, i.e., April, July and October.

CHANNEL SITES

At each of the six channel sites the following information was collected:

Salinity of the water. At each site three surface samples were taken from points 10m apart along the channel. The salinity of the water was determined in parts per thousand using a refractometer.

Fish and nektonic invertebrates. At each site a blocking net (3mm mesh) was thrown across the channel at two points a measured distance apart (appoximately 8m). The nektonic organisms trapped between the nets were caught by dragging a hand net (1mm mesh) through the water several times (usually 5 to 10 times) until no more were caught. [This was a laborious task at most sites because of the abundant macroalgae.] The fish and other organisms were then identified, counted and released. Specimens that were difficult to identify in the field were preserved in 70% alcohol for later examination in the lab.

Birds. At each site a 200-m portion of the channel was censused by walking along the bank and counting all the birds that occurred in the channel. These censuses were conducted each month.

The channel bottoms consist of three microhabitats: the high intertidal mud, the mid-to-low intertidal mud and the mid-channel mud. When collecting the following benthic information we made three measurements, one in each of the microhabitats, and between 1m and 2m apart.

Depth of anaerobic layer. At each site one hole was dug in the sediment in each microhabitat and the depth of the aerobic-anaerobic boundary was measured.

Macroalgae abundances. At each site one circular quadrat (56cm diameter = 0.25m^2) was placed in each microhabitat. The drifting macroalgae in each quadrat were collected, most of the water squeezed out of it and weighed.

Benthic invertebrates. At each site one coffee can corer (10cm diameter x 14cm tall) was pushed 12cm into the sediment in each microhabitat. The core was removed and the sediment was washed over a 1-mm screen. The residues were then preserved in 70% alcohol. All macrofauna in the residues were identified and counted under a dissecting microscope.

"MARSH" SITES

Each marsh site is a permanently marked square plot, 15m x 15m. The northeast and northwest corners of the square are marked by a black stake and a blue stake, respectively. Each stake has an aluminum label attached to it with PERL and SITE # written on it. At each of the marsh sites the following information was collected:

Soil moisture, soil salinity and soil nitrogen. At each site three randomly placed soil cores were obtained using a 2-cm diameter corer. The soil (approximately 100g) from the 5 - 15-cm depth was bagged, put in a cooler and returned to the lab where it was frozen for later analysis. Each soil sample was divided into three portions. The first portion was weighed, dried for 24 hours at 80°C, reweighed, and the percent moisture content (C) was computed as: $C = 100[(W - D) / D]$, where W is the sample weight wet and D is the sample weight dry. The second portion was thoroughly mixed with de-ionized water until the paste was runny (soil paste, cf. Richards 1954); the salinity of the interstial water was then measured in parts per thousand using a refractometer. This technique estimates the salinity of the soil after a heavy rainfall (PERL 1990). Finally, the extractable nitrogen of the third portion of the soil sample was measured by extracting the soil in 50ml of 2M KCl for an hour and analysing the extract for NH_4 using the automated phenate method and for (NO_3 + NO_2) using the cadmium copper reduction method. In this report we give the results as total extractable nitrogen in the soil, i.e. $NH_4 + NO_3 + NO_2$.

Algae. At each site the abundance of algae was estimated by randomly placing three circular quadrats (56cm diameter) in the site and estimating the percent cover in each quadrat.

Standing crop of the vascular plants. At each site the maximum canopy height was measured at three places selected haphazardly. In addition, we collected plants during August to estimate the end of year biomass at each site. Three 35-cm diameter quadrats were randomly placed in each site. The plants within each quadrat were clipped at ground level, bagged and returned to the lab where they were separated into species, dried at 75°C for two days and weighed.

Nitrogen content of *Salicornia virginica* foliage. At each site where *Salicornia* occurred (Sites 7 to 15) one sample of green *Salicornia* foliage (approximately 20grams) was collected from more than five plants. The sample was bagged, put in a cooler and returned to the lab where it was frozen for later analysis. Each sample was dried at 80°C to a constant weight, ground in a Wiley mill, and digested by the Kjeldahl method. The digest was analysed for total nitrogen.

Detritus production. Detritus production was estimated by placing three plastic trays in each of the sites. (Plant pots 18cm in diameter and 3.5cm deep were used.) The trays were placed flush with the surface of the soil, and left for 28 days, after which the accumulated debris was weighed.

Decomposition rates. Decomposition rates were measured using *Scirpus californicus*. Although *Scirpus* is not abundant in Ballona Wetland, it is a useful plant to use in decomposition comparisons because similar green plants can be collected during each season and the type of plant material can be relatively constant from season to season, and from year to year. *Scirpus* was collected from PERL at Tijuana Estuary; stems were cut into 25-cm lengths and dried for 2 days at 75°C. Approximately 40g of the plant material was placed in a 5-mm mesh bag and weighed. Three of the bags were randomly staked on the soil surface in each of the sites and left for 28 days. The litterbags were then bagged and returned to the lab where they were redried at 75°C for 2 days and reweighed. The difference in the before and after weights is a measure of the decomposition rates at Ballona Wetland.

Invertebrates. The marsh invertebrates were sampled in two ways. First, small mobile invertebrates, principally spiders and insects, were sampled using pan traps. (Plant pots 18cm in diameter and 3.5cm deep were used.) Three traps were randomly placed in each site. They were placed flush with the surface of the soil, filled with propylene glycol (anti-freeze) and left for 48 hours; the propylene glycol was then strained through a 0.5-mm mesh screen and the organisms caught were preserved in 70% alcohol and later identified (mostly to family) and counted under a dissecting microscope. Second, large organisms were sampled using a circular quadrat (56cm in diameter, $0.25m^2$ area). Three quadrats were randomly placed in each site and the large animals (primarily snails) in the quadrat were counted.

Birds. At each site a 200 x 25m strip (1/2 hectare) was censused by walking a path near the site and counting all the birds that occurred on the ground or in the vegetation in the strip; species that flew over the habitat or were observed in the habitat but out of the strip were noted as "also present." All censuses were conducted between sunrise and three hours after sunrise. Censuses were conducted each month.

Red Foxes. All foxes seen during visits to the wetland were counted and their locations noted.

RESULTS AND DISCUSSION

The period of study coincided with a below-average rainfall year. As in the previous three years, there was little wetting of the site by rainfall and no naturally-occurring flood event.

CHANNEL SITES

Tidal range and current speeds. There was little tidal flow in the channels. On most days the difference between the depth of the water at high and low tides was only a few centimeters. On 11 January 1990 the predicted high and low tides for the open shore were 7.3ft and -1.7ft (2.2m and -0.5m) MLLW respectively, for a tidal amplitude of 9ft (2.7m) -- one of the highest tidal ranges of the year. The tidal range was measured at the six channel sites on that day to estimate the maximum tidal range in the channels. The tidal range was less than 1m inside the Ballona Wetland (Figure 4A); it was greatest in the channels close to Ballona Creek (at Site 1) and dropped off rapidly away from Ballona Creek. On a similar day current speeds were measured during the ebbing tide. Maximum flow rates were generally low; they ranged from 0 (Site 6) to 17m/minute (Site 4), and averaged 4.6m/minute in the other sites.

Water salinities. The salinity of the water varied from seawater (35ppt) at Site 1 to fresh water (0ppt) at Site 6. The average salinities were higher at Sites 1 through 4 indicating that these sites were most influenced by Ballona Creek, where the salinity is usually near that of seawater. The average salinities were lower at Sites 5 and 6, the sites farthest from Ballona Creek, indicating that these sites were more influenced by the freshwater runoff into Ballona Wetland (Figure 4B).

In late summer 1990, there was an unusual discharge of freshwater into Ballona Wetland. This water came from a dewatering project upstream that discharged 500gal of water/min for 24hours/day for three months, i.e., from August through October (Victor Leipzig, personal communication). One effect of this freshwater discharge was to lower the salinity greatly at all sites; whereas the average salinity in the channels had been 35ppt in July it was only 5ppt in October (Figure 4C). Without this unusual inflow, it is likely that the average salinity would have remained at approximately 35ppt from July until the first big rain storm, which came during November this year. We believe that this unusual discharge of freshwater into the system during summer and fall had a detrimental effect on the organisms living in the channels (see below).

Macroalgae. Macroalgae, primarily *Enteromorpha*, were abundant at all channel sites except Site 6 (Figure 5A). At Sites 3, 4 and 5, the macroalgae were so abundant that they covered more than 85% of the channel bottom and the average wet weight was more than 300g per quadrat or 1200g per m^2. The average wet weight of algae in the channels increased from spring (174g per quadrat) to summer (297g per quadrat) to fall (341g per quadrat). We hypothesize that macroalgae were so very abundant at Ballona Wetland because (a) the slow current speeds allowed them to accumulate, and (b) inflows from urban areas and from the old agricultural fields stimulated growth. These hypotheses are not mutually exclusive and both may describe the current conditions at Ballona Wetland. The restoration of tidal flow should decrease the abundance of macroalgae by increasing current speeds and by reducing the influence of urban and agricultural inflows.

Depth of anaerobic layer. The depth of anaerobic/aerobic boundary averaged for all microhabitats and sites was 0.2cm below the surface of the sediment, i.e. very shallow.

Benthic invertebrates. Benthic invertebrates were common at Sites 1 to 3 only (Figure 5B). Particularly abundant at these sites were crabs (during summer), Spionid worms, Capitellid worms and the snail, *Cerithidea californica*. [Detailed results are given in Appendix 1.] The generally low abundances of benthic invertebrates at Sites 4 and 5 may be due to smothering by the abundant macroalgae at these sites.

The benthic invertebrates were less than half as abundant during October as they had been during April and July. For instance, at Site 1 there was an average of 35 individuals per core during July but only 13 individuals per core during October (Appendix 1). We hypothesize that the unusual freshwater discharge into Ballona Wetland, described above, caused this decline, either indirectly through the growth of smothering macroalgae or directly. Experimental work on the impact of low-salinity shocks has shown that several estuarine invertebrates are quickly killed by freshwater treatments (Stacey Baczkowski, PERL, pers. comm.).

Fish and nektonic invertebrates. Nektonic insects, mostly water boatmen, were abundant only at Site 1 (Figure 5C). Fish occurred at all sites; but were most common at Sites 5 and 6 where many mosquitofish were caught (Figure 6A; Appendix 2). Crayfish were abundant only at Site 6. The distributions of these nektonic organisms appears to be due to their searching out areas of preferred salinity. Support for this comes from a seasonal comparison of their distributions. The species most common at Sites 1 and 2 during April and July (e.g., topsmelt, water boatmen) when the salinities there were relatively high, were rare there during October when the salinities were very low. On the other hand, the mosquito fish appears to search out waters of low salinity; it was common at Site 5 and absent from Sites 1 and 2 during April and July, but it appeared in all habitats during October when the salinities everywhere were low (Appendix 2).

The fish community at Ballona Wetland is similar to the communities found in channels of salt marshes elsewhere - i.e., dominated by topsmelt, longjaw mudsucker, arrow goby, California killifish, and mosquito fish (Nordby and Zedler, in press). However, there are generally fewer fish species and fewer fish individuals at Ballona Wetland. We suggest four reasons for this. First, greatly lowered salinities can kill estuarine fish (Chris Nordby, pers. comm.). Second, there was sometimes little water in the channels for the fish; Site 6 tended to dry out during summer, and during very low tides Sites 1 through 4 were almost dry -- the fish were forced to retreat with the tide into Ballona Creek or seek out the few pools that were available to them. The only channel that always had water in it, Site 5, also had the most fish in it (Figure 6A). Third, macroalgae appear to smother the benthos and reduce the prey available to carnivorous fish. And finally, the anoxic sediments may give off enough sulfides to be toxic to fishes (Russ Vetter, NMFS Southwest Fisheries Lab, pers. comm.).

Birds. Birds were rare in the channels; none of the sites averaged more than 2 birds per 200m of channel (Figure 6B). The birds that did occur included herons (e.g., Great Egret, Black-crowned Night Heron), shorebirds (e.g., Killdeer, Willet), ducks (e.g., Mallard, Blue-winged Teal) and passerines (e.g., Red-winged Blackbird; Appendix 3). We hypothesize that birds were rare because their foods, particularly fish and benthic invertebrates, were rare.

"MARSH" SITES

Soil salinity. The soil salinities were low in the old agricultural fields (Sites 19 - 21), moderate in the *Salicornia* dominated marshes (Sites 7 - 15), and high in the salt pannes (Sites 16 - 18; Figure 7A).

Soil moisture. The moisture content of the soil was highest in the western-most sites (Sites 7 - 10) and declined toward the east; moisture content was very low in the old agricultural field sites (e.g., Site 19; Figure 7B). The marsh sites were generally drier than marsh sites in other southern California estuaries. One consequence of this dryness is that algae were very rare in the Ballona Wetland marshes. An algal mat, dominated by *Enteromorpha*, occurred only in Site 8, the wettest site.

Nitrogen content of the soil. The soils at Ballona Wetland were high in inorganic nitrogen. Total nitrogen values for other salt marshes are generally less than 10 micrograms of total extractable nitrogen per gram of dry soil (Zedler et al. 1990), but at Ballona Wetland four sites had values higher than 15 micrograms of total extractable nitrogen per gram of dry soil (Figure 7C). We hypothesize that fertilizers used in the old agricultural fields have leached into the salt marsh and salt panne soils. Further, it appears that differences in the drainage of the agricultural fields can account for the spatial patterning of very high and moderately high soil nitrogen. We suggest that the relatively good drainage south of Culver and Jefferson has flushed the nitrogen out of that system and today the nitrogen content of the soils at Sites 21, 15 and 14 is relatively low. On the other hand, the relatively poor drainage north of Culver and Jefferson has not allowed the nitrogen to be flushed out of that system and today the nitrogen content of the soils at Sites 13, 16, 17, 18, 19 and 20 is remarkably high.

Vascular plant community. *Salicornia virginica*, pickleweed, dominated at Sites 7 to 15 whereas "other species," e.g., grasses, *Bassia hyssopifolia*, *Salsola iberica*, *Rumex sp.*, *Cressa truxillensis*, dominated at Sites 19 - 21. Soil salinity can explain why the species composition varies from site to site; "other species" occur where the salinity is less than 6ppt, *Salicornia* occurs where the salinity is between 7ppt and 30ppt, and no plants occur in areas where the salinity is over 40ppt, i.e., in the salt pannes (Figure 8A).

Standing crop of the vascular plants. The end-of-year biomass ranged from zero in the salt pannes (Sites 16 to 18) to 300g dry weight per quadrat ($1/10m^2$) at Site 10 (Figure 8B). Relative to other southern California wetlands that have abundant *Salicornia*, Ballona Wetland had very high aboveground biomass of *Salicornia virginica* (Table 1). Comparing all the sites for which we have data on pickleweed biomass, there is a general pattern of higher standing crop in areas that are not continuously tidal. Peñasquitos Lagoon, a semi-tidal wetland in San Diego County, had the highest value on record in 1978, a flood year with major freshwater inflow. During drier years (e.g., 1977) the standing crop at Peñasquitos Lagoon was similar to that at Ballona Wetland. At two tidal estuaries, Mugu Lagoon and Tijuana Estuary, pickleweed standing crops were generally lower than at Ballona Wetland (Table 1).

Canopy height. The maximum canopy heights ranged from 26cm to 73cm in the *Salicornia* marshes at Sites 7 to 15 which is generally taller than *Salicornia* marshes in tidal, Tijuana Estuary (PERL, unpubl. data). The *Salicornia* canopy heights changed little from season to season (i.e., small std errors; Figure 8C). On the other hand, the canopy heights varied considerably in the old agricultural fields (Sites 19 - 21). Here the vegetation was a mixture of various annuals (e.g., grasses, *Bassia hyssopifolia*, *Salsola iberica*, *Rumex sp.*, *Cressa truxillensis*) that were relatively short in April, but by October were more than 1m tall in most places. There was no vegetation in the salt panne sites (Sites 16 - 18).

Maximum canopy heights were also measured when the end-of-year biomass data were collected. A comparison of maximum canopy height and total biomass shows that the *Salicornia* at Sites 7 to 15 followed a different pattern to the "other species" at Sites 19 to 21 (Figure 9A). *Salicornia* appeared to reach a threshold height at approximately 55cm; sites with relatively high biomass were no taller than sites with relatively low biomass. Therefore for *Salicornia* one cannot predict biomass from maximum canopy heights. On the other hand, the line for the "other species" is quite a good fit -- the "other species" did not reach a threshold and one can predict biomass from maximum canopy heights. Notice that even though the *Salicornia* was generally shorter than the "other species" its biomass was generally greater (Figure 9A).

Foliage condition. Most of the biomass of pickleweed exists as brown, rather than green branches (Table 1). Although values were spatially variable at Ballona Wetland, most sites had less than 20% green material. Site 15 had the highest proportion of green biomass, but total biomass was very low, apparently in part due to insect damage (Boland, pers. obs.). Low percentages of green branches have also been found at Mugu Lagoon. In August, when green branches were at their peak biomass, they comprised only 29% of the total aboveground material; from October through February, green branches were below 10% of the total (Onuf 1987).

Foliar nitrogen of the vascular plants. The *Salicornia* foliage was high in nitrogen. The range at Ballona Wetland was from 18.6 to 26.8mg nitrogen per gram of plant material (Figure 9B), whereas the range for four recently sampled *Salicornia* sites at Tijuana Estuary was from 6.2 to 10.2mg N/g (Zedler et al. 1990).

High foliar nitrogen concentrations might arise either from a high proportion of nitrogen or a lower salt load in the plant tissue. In other words, plants from the two estuaries could have different C:N ratios, and different protein content; or the plants could have similar C:N ratios but different concentrations of nitrogen per dry weight, if those from one site have a higher salt content.

Evidence that Ballona Wetland has higher nitrogen availability than Tijuana Estuary is provided by the nitrogen content of the soil, which ranged from 2.5 to 23.4 mg/kg at Ballona Wetland (Figure 7C) and from 1.7 to 16.0 mg/kg at Tijuana Estuary. However, Covin and Zedler (1988) show that nitrogen-loading rates, rather than inorganic N concentrations in soils are the critical determinant of plant growth, and such information is very difficult to obtain. The suggestion that plants at Ballona Wetland may have lower salt content than those at Tijuana Estuary follows from the lower soil salinities at Ballona Wetland. However, we lack information on ash-free dry weights or C:N ratios for *Salicornia virginica*. A CHN analyzer will soon be available to PERL to allow such analyses in the future.

Detritus production (litter fall). Material falling from the canopy averaged less than 2g per pan per month in all sites (Figure 9C). Although these monthly rates appear low they are for approximately 1/40 square meter and for 1/13 of a year. Averaging the measurements for Sites 7-15 for all three measurement periods and extrapolating values to a full year indicates 400g/m^2/yr litter fall for Sites 7 to 15.

Vascular plant decomposition. Loss rates of plant material *(Scirpus californicus)* from litterbags were low, especially considering that the data are for the first four weeks of decomposition. The rate of loss during the 28 days averaged 4.4% for Sites 7 to 15 (Figure 10A). The lowest loss rate was 2.1%/month at stations 14 and 15 in July, and the highest loss rate was 10.3%/month at station 8 in October (Figure 10A). Material deployed in July (mean 2.4%/month) was slower to decompose than that deployed in spring (5.1%/month) and fall (5.6%/month).

In April 1988, Rutherford (1989) deployed litterbags of *Spartina foliosa* in low and high marsh sites at tidal marshes along San Diego Bay. Her average first-month decomposition rate was 42%/month, with a range of 39 to 45%/month. The decomposition rates at San Diego Bay are therefore much higher than at Ballona Wetland. Because the San Diego Bay and Ballona Wetland studies used different species and took place in different years, the comparison is only a general one. However, it is the expected difference, since drier sites are known to have slower decomposition rates (Winfield 1980).

Invertebrates. The invertebrates caught in the pans were primarily amphipods, spiders and insects (particularly Collembola, Diptera, Homoptera, and Hymenoptera; Appendix 4). There were a moderate number of invertebrates (approximately 60 per pan) at most sites, but more invertebrates were caught in the wetter *Salicornia* sites (Sites 7 to 9) than in the drier *Salicornia* sites (Sites 13 to 15; Figure 10B). The invertebrate community at Ballona Wetland was similar to the communities in tidal estuaries (PERL 1990). The African land snail, *Otala lactea*, occurs in the wetland; it was common (approximately 1 per m^2) at Site 19 and present (<1 per m^2) at Sites 10 - 15, 20 and 21. It was particularly obvious on wet mornings.

Birds. Birds were rare at most sites except the old agricultural fields and Sites 11 and 17 (Figure 10C). The most common species were the Savannah Sparrow and Western Meadowlark in the *Salicornia* sites (Sites 7 to 15); the Great Blue Heron and Blackbellied Plover resting in the salt panne (Site 17); and the Savannah Sparrow, White-crowned

Sparrow, and House Finch in the old agricultural fields (Sites 19 to 21; Appendix 5). Although Savannah Sparrows occurred in all habitats, males set up breeding territories near Site 11 only. We observed a maximum of nine males displaying in this area (during March). Other species that showed breeding behavior and were likely breeders in the wetlands were the Killdeer, Western Meadowlark and Red-winged Blackbird.

Foxes. Red Foxes breed in the wetland - there was a fox den near Site 11 -- and individuals were seen in the wetland during every visit. The greatest number -- eight -- was seen on 23 April; four of these individuals were adults (seen near Sites 10, 11, 12, and 14) and the other four were cubs (frolicking with an adult at the den). Fox counts made during the monthly bird censuses are given in Appendix 6.

GENERAL DISCUSSION

The aims of our research are to test ideas about the functioning of southern California's coastal wetlands and to provide information that will improve the restoration effort. The research done in 1990 is the first half of the complete study -- i.e, the before-restoration condition at Ballona Wetland. We have presented the detailed results of our 1990 field research; now we discuss four general topics: the significance of the high pickleweed standing crop, the Belding Savannah Sparrow's choice of breeding habitat, restoration problem areas, and the nature of the food webs at Ballona Wetland before tidal restoration.

The significance of the high pickleweed standing crop. The high standing crop of pickleweed at Ballona Wetland does not necessarily mean that there was high pickleweed productivity, nor does it necessarily indicate high functional value. On the contrary, two systems with low pickleweed standing crops, Mugu Lagoon and Tijuana Estuary, were considered to be the region's most natural ecosystems in 1976 when the California Sea Grant College funded basic research at each site.

Pickleweed is a highly variable species; it has a very wide geographic range, has the broadest intertidal range of all the salt marsh natives, can dominate both tidal and non-tidal sites, and has a variety of growth forms. It is also a rather brittle plant, that readily loses branches when disturbed. In non-tidal areas, branches often grow thicker, and biomass accumulates because it is neither transported out of the system nor decomposed in situ. In fully tidal sites, there is less biomass accumulation, because tidal flows cause breakage, facilitate decomposition, and export plant parts.

The functioning of the pickleweed might be characterized by calculating a "turnover time," defined here as the August biomass/annual aboveground productivity. At the tidal Mugu Lagoon, Onuf (1987) estimated the annual aboveground productivity to be 290 g/m^2, for a turnover time of 440/290 = 1.5. This suggests that every 1.5 years, the material in the canopy is completely renewed, or that the average stem lives 1.5 years. Even though the pickleweed productivity rate is not very high, the system would be considered very dynamic, with much material being removed from the canopy, rather than accumulating.

At Ballona Wetland, the turnover time cannot be calculated, because we did not set out to measure plant productivity (the effort required greatly exceeded available funding). However, we can use some of our results to speculate on the dynamics of pickleweed at Ballona Wetland. If we assume that Ballona Wetland had the same productivity rate as at Mugu Lagoon, the turnover rate would be estimated as 1372/290 = 4.7. Our data on detritus production rates suggest that Ballona Wetland productivity was slightly higher than that measured at Mugu Lagoon. For the plant canopy to remain constant in biomass, net aboveground productivity would need to be about equal to the litter fall (detritus production) rate we estimated (400g/m^2/yr). With a productivity rate of 400g/m^2/yr, the turnover rate would be estimated as 3.4 years.

We believe that Ballona Wetland had a somewhat higher pickleweed productivity rate and a somewhat longer turnover time than Onuf found at the lower marsh of Mugu Lagoon. High vascular plant productivity rates are certainly possible for semi-tidal systems. The earlier comparisons of Tijuana Estuary and Peñasquitos Lagoon provided strong indications that pickleweed may be more productive with reduced tidal flushing, and Griswold's (1988) data indicated that it grows better when not in continually saturated soils (Table 1). We also suspect that turnover rates differ for semi-tidal and tidal systems. The high standing crops at Ballona Wetland and Peñasquitos Lagoon surely indicate longer turnover times for the plant canopy in semi-tidal estuaries.

The Belding's Savannah Sparrow's choice of breeding habitat. The Belding's Savannah Sparrow is an endangered species that occurs in Ballona Wetland year round. In 1989 and 1990 Massey and Corey found between nine and 31 male breeding territories in the wetland (PERL 1989, Corey and Massey 1990). Although Belding's Savannah Sparrows were seen in other habitats during the breeding season (Appendix 5), in both years they established breeding territories in and around Site 11 only (Boland, pers. obs.; Corey and Massey 1990). Because much of the habitat around Site 11 is at a low elevation, it is likely that much of the current sparrow breeding habitat will be lost after tidal restoration (PERL 1989). Therefore some important questions need to be addressed: Why did the sparrows choose to set up breeding territories at Site 11 only? And can habitats elsewhere be improved so that the sparrows will move there when tidal flow is restored?

Let us tackle the first question, i.e., why did sparrows choose to set up breeding territories at Site 11 only. Corey and Massey (1990) do not address the question directly but imply that the general dryness of the marsh has limited the birds to this habitat. In previous years, e.g., 1987, there were 29 territorial males near Sites 7, 8, 10, 11, 12 and 18. The sharp reduction in the number of territorial males from 1987 to 1989 they say "is thought to be the end result of lack of tidal flow and the long drought that southern California has been experiencing over the past four years." We may call their idea for why the sparrows are now in this site only: The Best Site in Dry Years Hypothesis.

However, our data indicate that Site 11 was not the wettest *Salicornia* site and did not support unusually large plants or many invertebrates. Sites 7 to 10 were wetter than Site 11 (Figure 7B), Sites 7 and 10 had greater plant biomass (Figure 8A), Sites 7 to 10 and 12 to 14 had greater canopy heights (Figure 9A), and all the other sites had more invertebrates (Figure 10B). So why did the territorial males choose Site 11 only? We suggest that they did it because it is the best site that is isolated from human disturbance. Three observations support this Isolation Hypothesis. First, we frequently saw people walking in the wetland near Culver Blvd. and near the west channel (i.e, near Sites 8, 9 and 14), often they were accompanied by dogs, but we never saw people near Site 11 -- it was too difficult to get to. Second, Belding's Savannah Sparrows have not set up breeding territories in other, apparently better, sites, i.e., where there was more vegetation cover and more invertebrates. Third, herons most frequently chose to rest in the salt panne near Site 11.

The important difference between these two hypotheses is that they provide different answers to the second question, i.e., can habitats elsewhere in Ballona Wetland be improved so that the sparrows will move there when tidal flow is restored? The Best Site in Dry Years Hypothesis suggests that when tidal flow is restored the sparrows will establish territories in other parts of the wetland. In contrast, the Isolation Hypothesis suggests that even if conditions do improve in other areas the sparrows will not set up territories there because there is too much disturbance. In fact the Isolation Hypothesis suggests that other areas of the marsh may already be better than Site 11.

We suggest that the managers take both of these hypotheses into consideration when developing the restoration plan. The plan should call for increased tidal flow into the marshes, increased restrictions to public access and creation and/or improvement of salt marshes in the most isolated parts of Ballona Wetland.

Restoration problem areas. We have noticed two areas in which the restoration of Ballona Wetland may have problems. The first concerns the restoration of Belding's Savannah Sparrow habitat -- and this problem has just been discussed.

The second concerns the actions of the Mosquito Abatement workers. First, there is conflict between the goals of the Mosquito Abatement District -- to drain flooded areas -- and the restoration of Ballona Wetland -- to allow the wetland to be wet. During February and March 1990, heavy rains flooded the *Salicornia* marsh near Site 15. Unfortunately Mosquito Abatement workers discovered mosquitoes in the water and so they sprayed the area around Site 15 with oil and dug a drainage ditch to lead the water into one of the channels. They also discovered mosquitoes in other parts of the wetland but because these wetlands are in areas they refer to as "the bird sanctuary" they used only a developmental hormone on these mosquitoes. Their actions appear to have been successful because by 23 March 1990 Site 15 was relatively dry and there were no mosquitoes remaining (Don Birkinshaw, pers. comm.). We believe that the Mosquito Abatement District need to be brought into the restoration program at Ballona Wetland. They should be asked to treat all areas as part of "the bird sanctuary," to drive on tarred roads only, and not to drain pooled areas.

The nature of the food webs at Ballona Wetland before restoration. We conclude that limited tidal flushing at Ballona Wetland has multiple impacts on both the structure and functioning of the wetland ecosystem.

Because of the low tidal amplitude, the linkages between the marsh and channel communities are limited. The two function more independently than in fully tidal wetlands. In a fully tidal system, the channel water flows into the marsh carrying channel organisms with it, and then flows out carrying marsh organisms into the channel. The result is that the distributions of marsh and channel species overlap and that movements between the two habitat types are facilitated. In addition, nutrients brought into the channels move onto the marsh and are taken up by the algae and vascular plants, and organic materials produced by the marsh algae and vascular plants move into the channels (Winfield 1980). In contrast, the limited tidal action at Ballona Wetlands severely restricts such interactions.

In the marsh, nutrient-recycling and food chain support functions are impaired. Detritus production and decomposition rates are both low, and pickleweed biomass accumulates, indicating slow recycling of plant material. Algal mats are rare or absent, limiting the grazer food chains that are thought to be very important in tidal salt marshes (Zedler 1980, 1982). Marsh invertebrate communities are dominated by spiders and insects indicating the terrestrial nature of the marsh food web. In addition, these invertebrates are relatively small and rare and therefore do not attract many birds.

In the channels, reduced salinities and poor water circulation have major impacts on the structure and functioning of the channel system. Macroalgae accumulate smothering the benthos; microalgae cannot grow; marine invertebrates are low in species richness and abundance; and birds and fishes are rare and low in species richness.

An additional consequence of reduced tidal flushing at Ballona Wetland is that exotic species -- both plant and animal -- have invaded the marsh and channel ecosystems. In the drier marsh sites, several weedy plants (e.g., *Carpobrotus* spp., *Atriplex semibaccata*) have become established in areas that would otherwise support native salt marsh vegetation. Such weedy invasions can reduce the growth of, or completely elliminate, native salt marsh plants (Zedler et al. 1990). Red foxes have established a den and reproduced within the salt marsh. In the channels, the exotic fish, the yellowfin goby, is present, and brackish marsh plants (e.g., *Scirpus robustus*) have encroached on the estuarine channels. These invasions are readily explained by two features of reduced tidal flushing -- the lower soil moisture of marsh habitats (which develop when high tides cannot inundate the site), and the lower salinities of marsh soils and channel waters (which develop when freshwater inflows are not "overwhelmed" by saline tidal waters).

RECOMMENDATIONS FOR FUTURE RESEARCH

Research to compare conditions before and after restoration.

The potential for restoration of tidal flows to Ballona Wetland has provided us with a unique opportunity to test several hypotheses about wetland ecosystem functioning. The general hypothesis (H1) and several specific hypotheses (H2-7) are outlined below. We have described the ecosystem in 1990 before restoration and need to conduct a long-term study after restoration to assess changes. The following hypotheses will be tested by repeating field sampling after the restoration is underway. It is not clear that the hypothesized changes will develop in the first few years of increased tidal flow. We recommend a 10-year montoring program of post-restoration ecosystem development, and strongly recommend that the 1990 sampling program be repeated annually for at least 5 years after tidal restoration. Should tidal enhancement occur over a period of years, the sampling should be extended appropriately.

H_1: Physical factors such as water salinity and current speeds in channels and soil moisture and soil salinity in marshes play important roles in controlling the nature of the food web in the estuary as a whole.

H_2: Channel macroalgae will decline following tidal enhancements because:
a) more rapid currents will prevent their accumulation, and
b) reduced influence of urban and agricultural inflows will lower growth.

H_3: The abundance of channel invertebrates and fishes will be higher and more stable with more predictable salinity regimes (i.e., elimination of non-seasonal freshwater intrusions).

H_4: Channel bird densities will increase because they are positively correlated with the densities of their fish and benthic invertebrate prey.

H5: After tidal flushing is enhanced, the salt marsh soils will support good pickleweed growth and high epibenthic algal productivity due to an abundance of soil nitrogen.

H6: After tidal flushing is enhanced, vascular plant standing crops will decrease and turnover time (standing crop/annual productivity) will decrease as breakage, export, and decomposition increase.

H7: Linkages between the marsh and channel ecosystems and food chains will increase in response to increasing tidal amplitude.

Additional research to be conducted before restoration.

Additional observations and experiments described below would advance knowledge of estuarine functioning in general, and of Ballona Wetland in particular. We believe that the more information the managers of Ballona Wetland have at their disposal the greater the chance that the restoration of Ballona Wetland will be successful.

First, continuation of our present study. We have completed three seasons of sampling at the 21 permanent study sites. Continued data collection through February 1991 would allow a full 4-season data set to chracterize the food webs before tidal enhancement. In addition, continued studies through February 1992 would be most useful because 1990 was not a typical before-restoration year. The unusual flow of freshwater into the Ballona Wetland channels from a dewatering project upstream severely lowered salinities in the channels, and we believe that it caused the dramatic changes in the abundances of macroalgae, benthic invertebrates and fishes in the channels. We recommend further studies before tidal enhancement to provide replication (and greater confidence in) the existing baseline data set.

Second, salt marsh primary productivity. We have been asked several questions about the importance of Ballona Wetland to the open water estuarine system of Ballona Creek. For example: How high is the primary productivity of the salt marsh? How will salt marsh primary productivity change with increased tidal flushing? Salt marsh primary productivity is difficult to measure; for vascular plants it involves monthly measurements of the growth of tagged branches (Onuf 1987) and for benthic algae it involves frequent measurements of the amount of oxygen evolved by mats placed in light and dark chambers (Zedler 1980). Both methods are problematical. We decided instead to measure vascular plant and algal standing crop. These results have revealed some interesting patterns, e.g., that the biomass of pickleweed is relatively high at Ballona Wetland, however our knowledge would be improved if we collected data on salt marsh primary productivity during 1991. We recommend these additional measurements to assess plant growth be made before tidal restoration for comparison after tidal restoration.

Third, foliar nitrogen concentrations. We found unusually high foliar nitrogen concentrations in the pickleweed at Ballona Wetland and identified two factors that could contribute to elevated tissue nitrogen: a lower carbon:nitrogen ratio in the plant's organic matter (and associated high protein content and high nutritional value) and/or a lower salt load due to lower-salinity soils. With the acquisition of a CHN analyzer and the opportunity to collect additional plant tissues for ash-free-dry-weight determinations, we can test for the relative importance of each factor in producing pickleweed with high nitrogen content. If the elevated foliar nitrogen levels are due to increased protein and nutritional values, Ballona Wetland may well have very high potential for food chain support, given additional tidal wetting. On the other hand, if the high N/plant weight is due to low salt content in the plant tissues, increased tidal flushing would quickly lower foliar nitrogen concentrations as marsh soils are flooded with seawater. We recommend sampling of pickleweed tissue and appropriate analyses (C:N content and ash-free dry weights).

Fourth, macroalgal experiments. We have hypothesized that macroalgae in the channels are smothering the benthos, promoting anoxic conditions near the sediment surface, decreasing the abundance of benthic invertebrates, and ultimately decreasing the abundances of fish and birds in the channels. We would like to conduct tests of these hypotheses in Ballona Wetland during 1991. The tests would involve removal of macroalgae from some sites in the western channel, the addition of macroalgae, or a suitable mimic (e.g., cloth pegged to the sediment), to some sites in the eastern channel, and the frequent measurement of the depth of the anoxic layer and benthic invertebrates in the study sites. We recommend that the impact of macroalgae on sediments be assessed.

Fifth, fish. Another question we have been asked regarding the importance of Ballona Wetland to Ballona Creek is: What role does the marsh system play in providing food chain support for the fishes in Ballona Creek? We could address this issue through the use of multiple stable isotopes. We could survey the marsh, channel, and ocean primary producers to obtain signatures for each potential source of plant foods. We could then look for a match in the signature of fish tissues to indicate whether various fishes are feeding primarily on marsh vascular plants, macroalgae, or phytoplankton. Unfortunately, the analyses for multiple stable isotope signatures are expensive, and a large number of samples would be needed to establish that linkages between Creek fishes and marsh producers exist. Other research on the fish in Ballona Creek should be done by local fish ecologists. If there is sufficient funding for and interest in establishing linkages between Ballona Creek and Ballona Wetland, we recommend a coordinated program of fish sampling and multiple stable isotope evaluation.

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Table 1. Comparative standing crop data for pickleweed *(Salicornia virginica)* in semi-tidal and tidal wetlands of southern California and for experimental (non-tidal) mesocosms. Data are for August standing crops (live + dead) in grams per square meter. The total green, total brown, and % green biomass data are also given. Sources are: this study for Ballona Wetland, Onuf (1987) for Mugu Lagoon, and Zedler et al. (1980) for Tijuana Estuary, San Diego River (flood control channel) and Los Peñasquitos Lagoon, and Griswold (1988) for experimental mesocosms.

Location	Site	Total	Green	Brown	% Green
Semi-tidal wetlands					
Ballona Wetland (1990)					
	western (#7-9)	**1928**	379	1549	18-22
	central (#10-12)	**2427**	247	2180	8-14
	eastern (#13-15)	**1372**	322	1050	16-51
Peñasquitos Lagoon	lower marsh				
1977		**2670**			
1978		**4415**			
Tidal wetlands					
Mugu Lagoon (mean for 1978-1981)					
	lower marsh	**440**	129	311	29
San Diego River	lower marsh				
1977		**799**			
1978		**1477**			
Tijuana Estuary	mid-marsh				
1976		**845**			
1977		**1096**			
1978		**956**			
Experimental mesocosms at PERL					
(1986-1987)	low elevation	**562**			
	medium elevation	**914**			
	high elevation	***2792**			

* Extremely variable; range of values among 9 mesocosms = 728-13,103).

Figure 1A. Simplified diagram of the existing food chains at Ballona Wetland. With minimal tidal influence, linkages between the channels and marshes are few. BSS = Belding's Savannah Sparrow. Box size is a crude indication of standing crop; width of arrow indicates relative amount of energy transfer (low vs. high rate). ? = uncertain transfer.

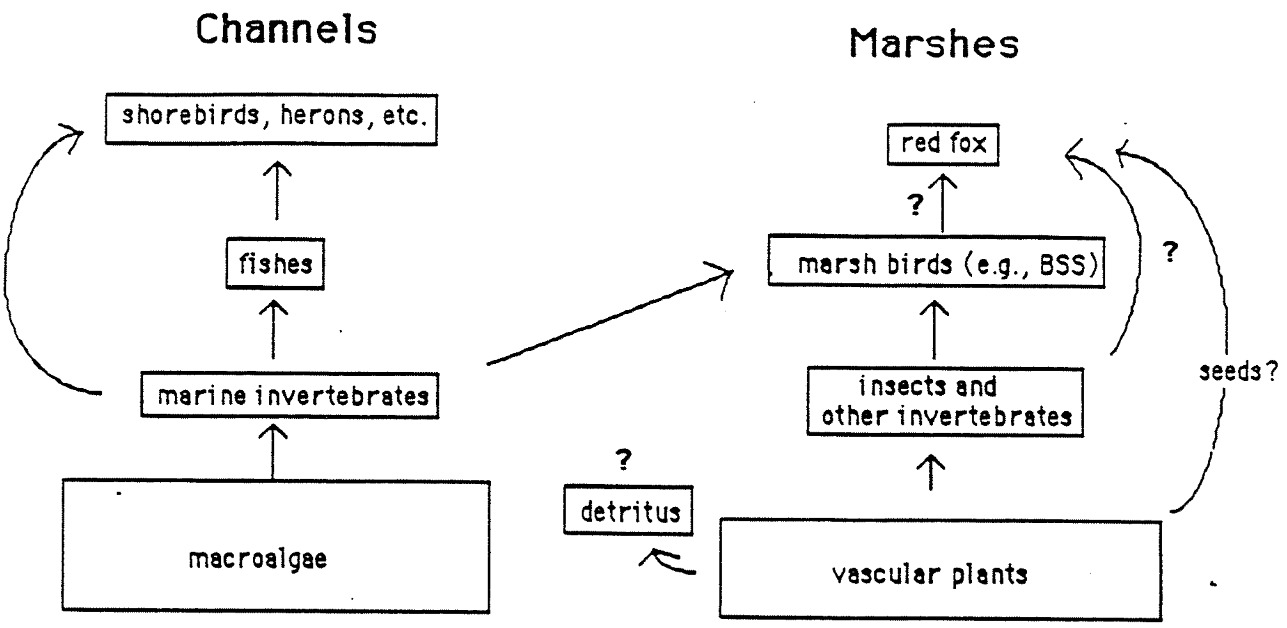


Figure 1B. Hypothesized food web at Ballona Wetland following tidal enhancement. With restored tidal flows, there would be many linkages between channel and marsh food chains.

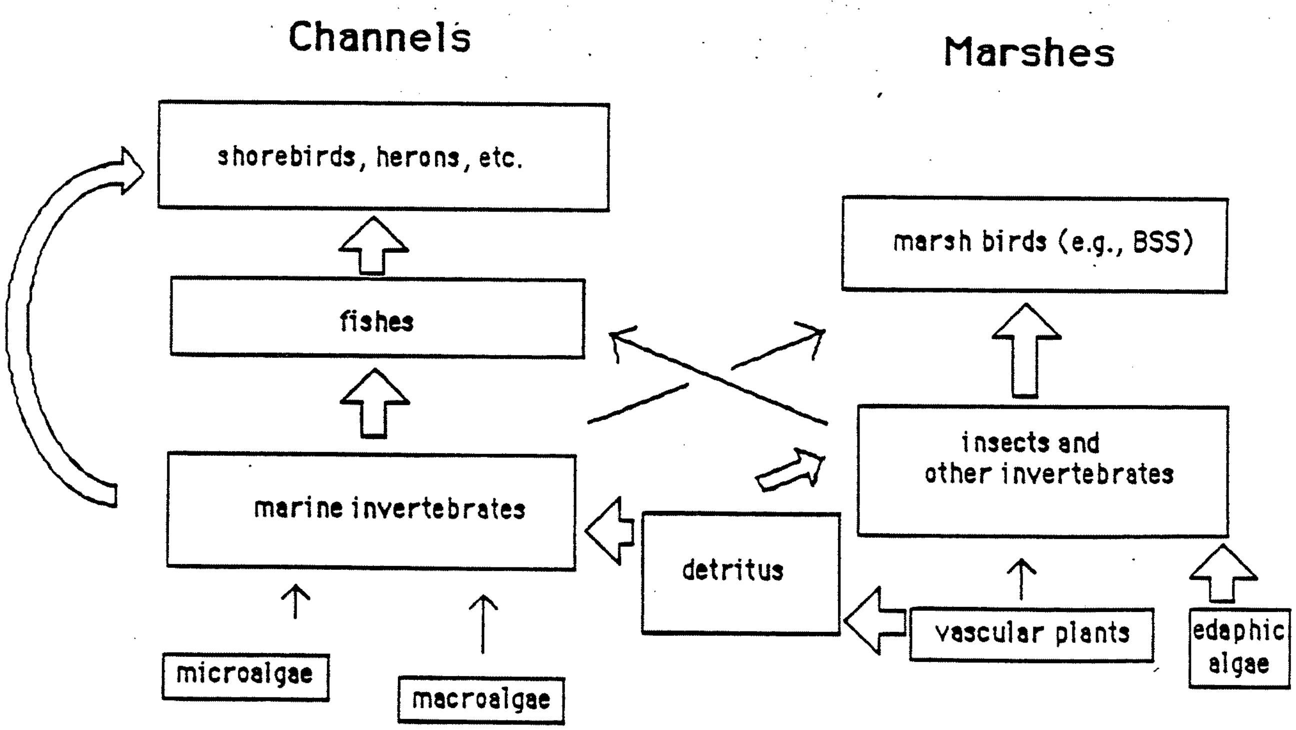
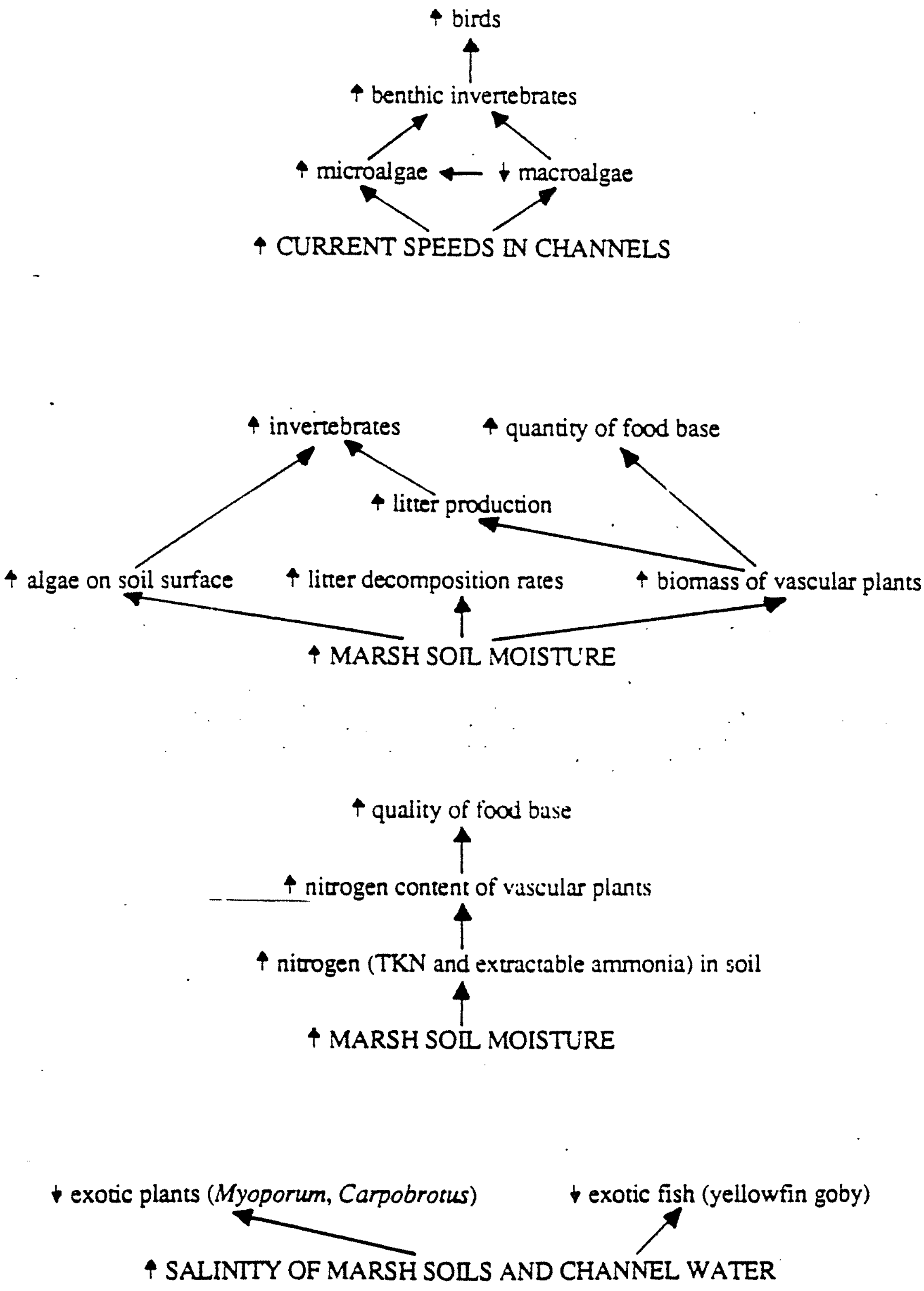
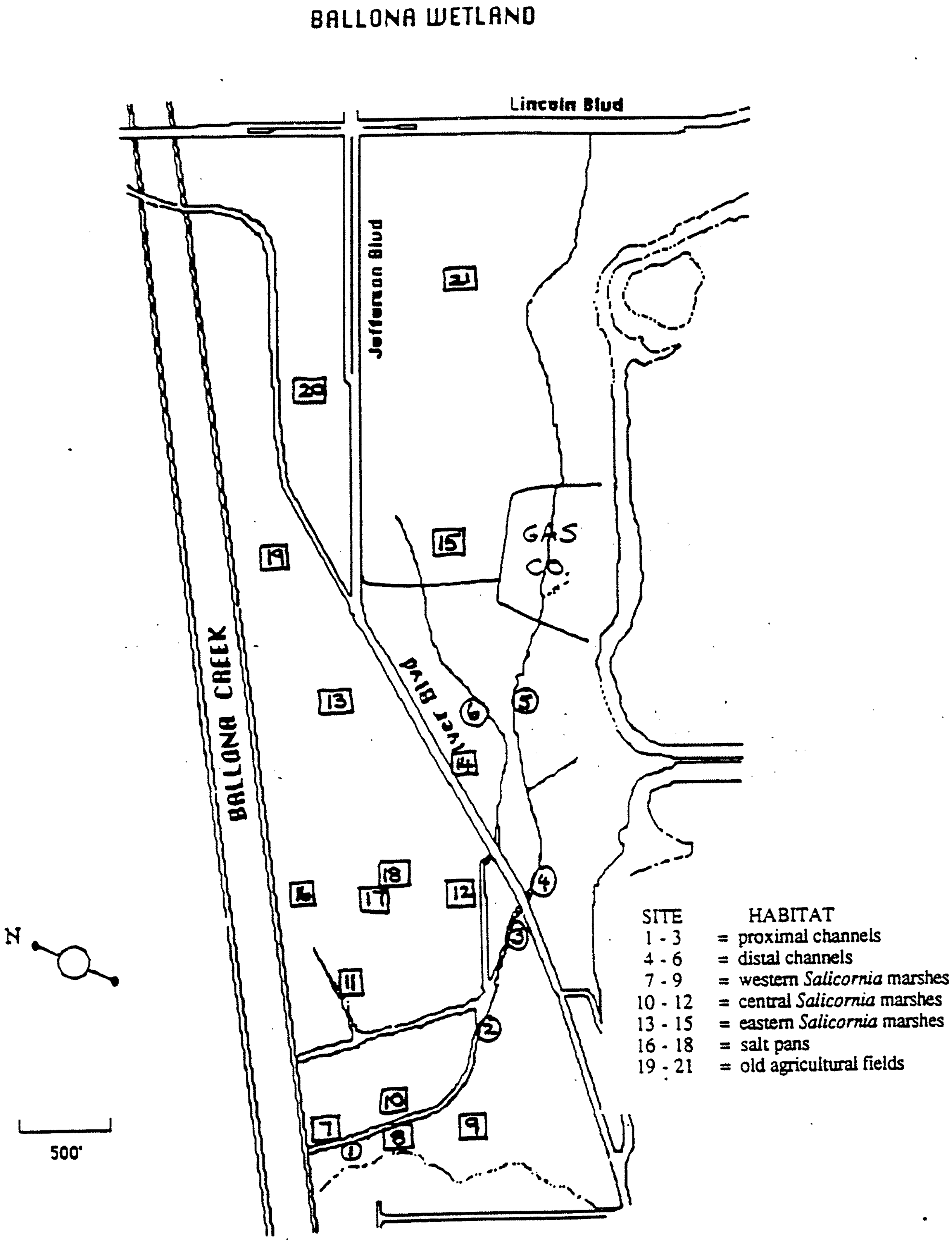


Figure 2. Hypothesized changes to environmental conditions and food chain support.





SITE	HABITAT
1 - 3	= proximal channels
4 - 6	= distal channels
7 - 9	= western *Salicornia* marshes
10 - 12	= central *Salicornia* marshes
13 - 15	= eastern *Salicornia* marshes
16 - 18	= salt pans
19 - 21	= old agricultural fields

Figure 3. The locations of the 21 sampling sites at Ballona Wetland.

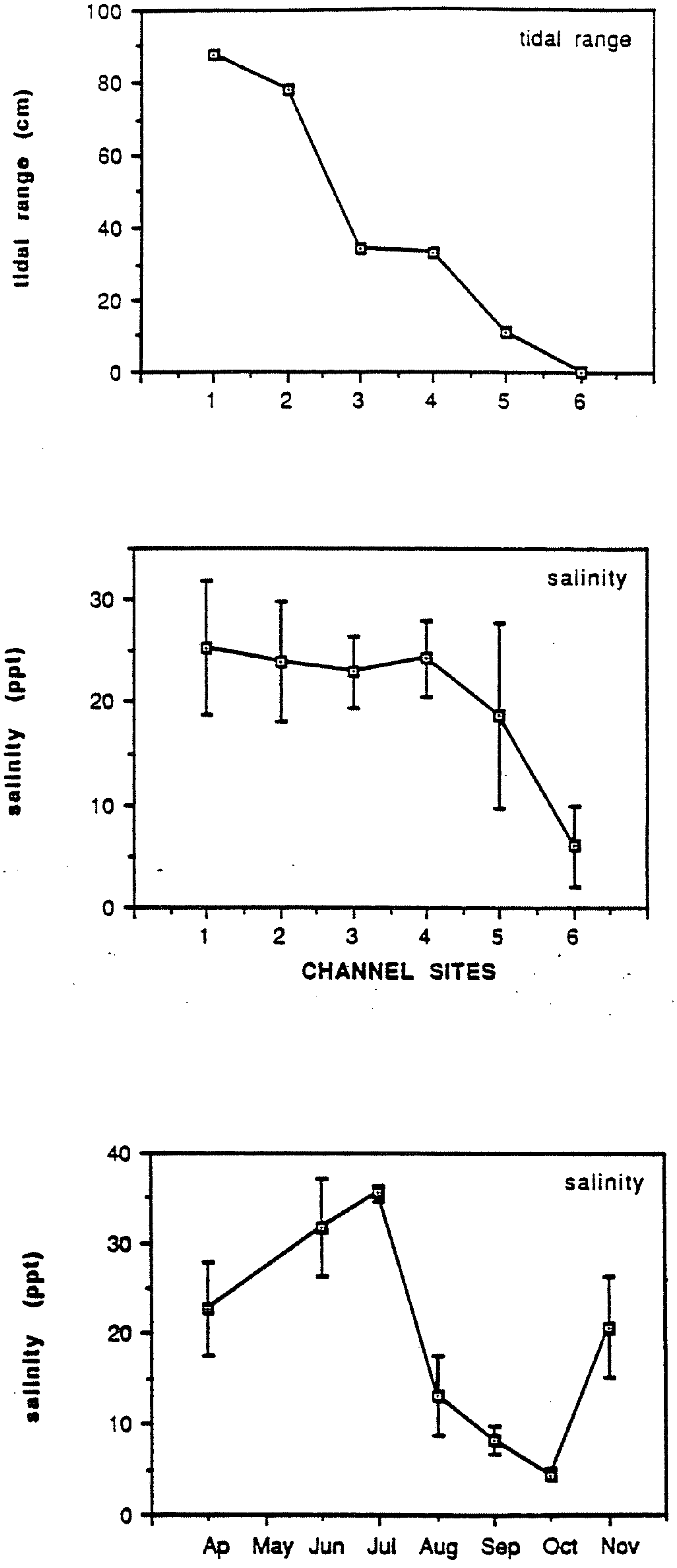


Figure 4. The magnitude of the tidal range (A) and the salinity of the water in the six channel sites (means of the three seasons ± 1 std. error; B). The sites are arranged in order of decreasing tidal amplitude. The changes in the salinity of the water in the six channel sites during the study period (means ± 1 std. error; C).

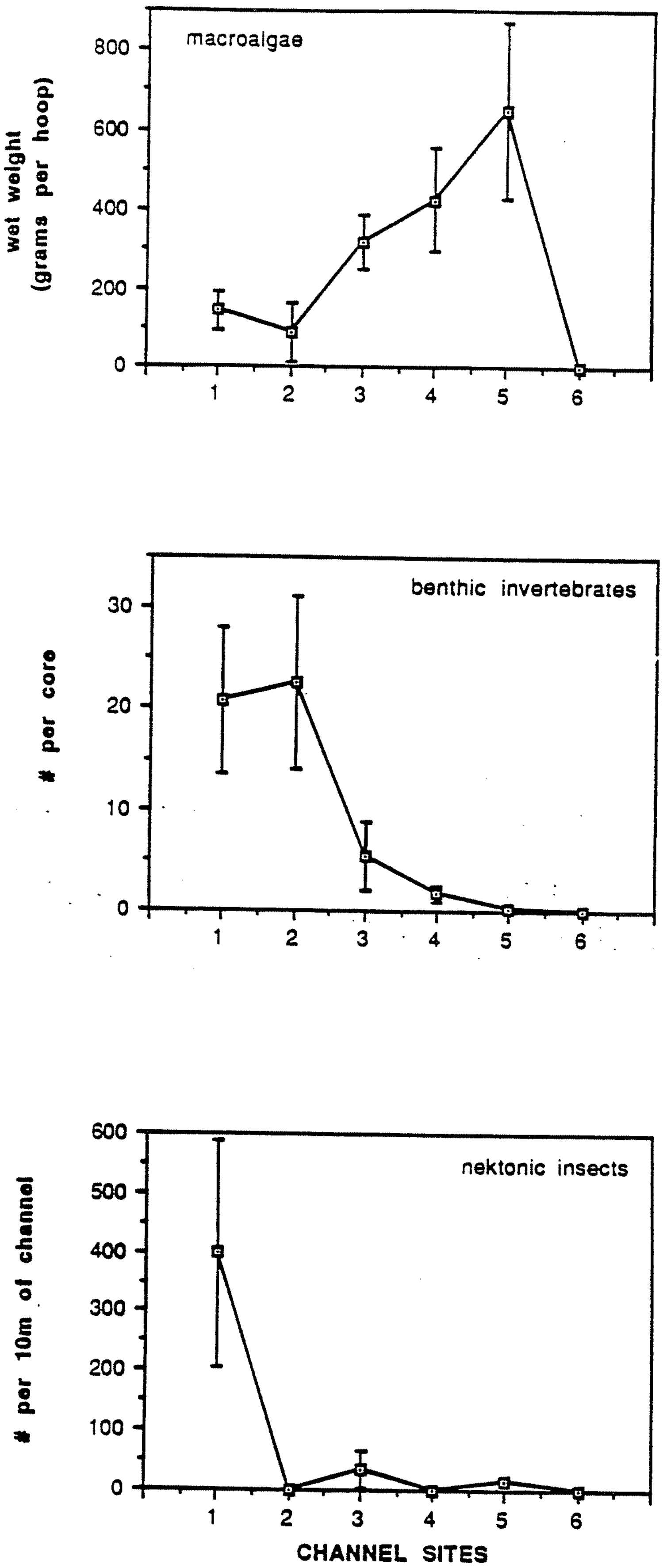


Figure 5. The abundances of macroalgae (A), benthic invertebrates (B), and nektonic insects (C) at the six channel sites (means of the three seasons ± 1 std. error). The sites are arranged in order of decreasing tidal amplitude.

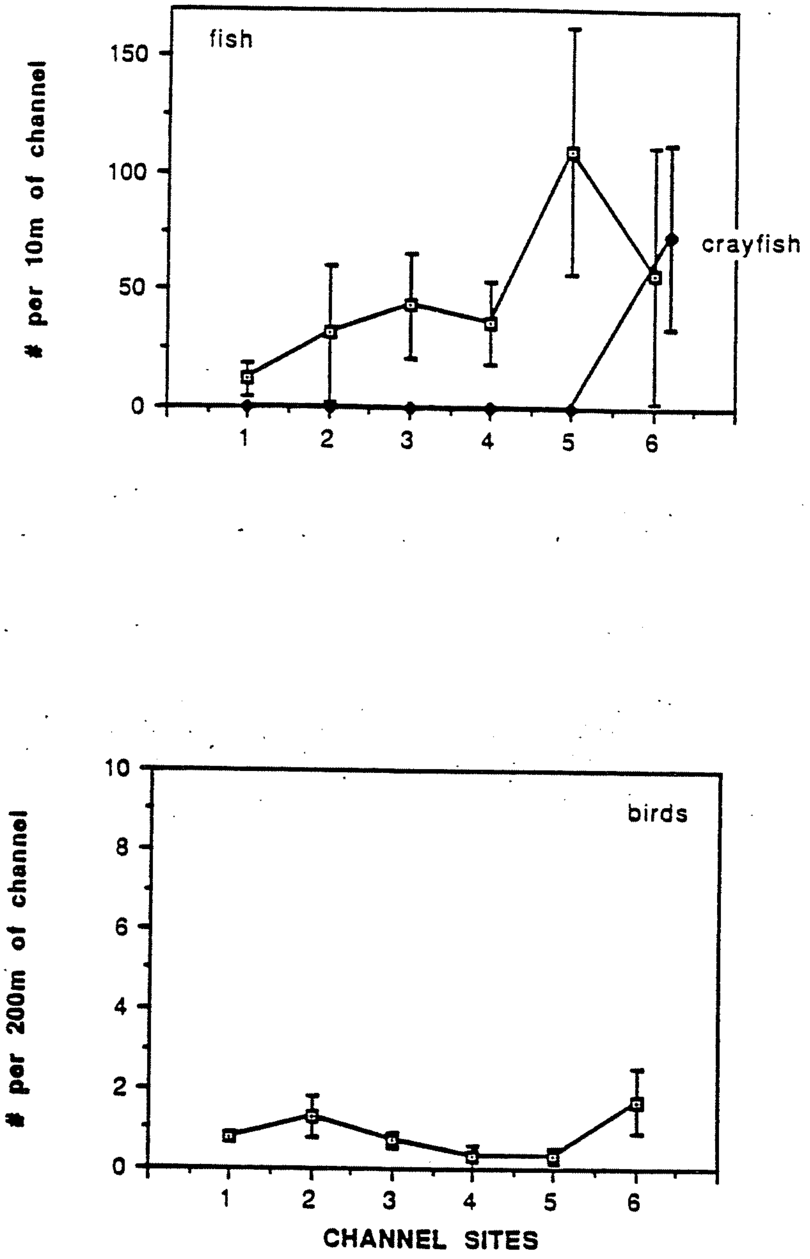


Figure 6. The abundances of fish (A), crayfish (A), and birds (B) at the six channel sites (means of the three seasons ± 1 std. error). The sites are arranged in order of decreasing tidal amplitude.

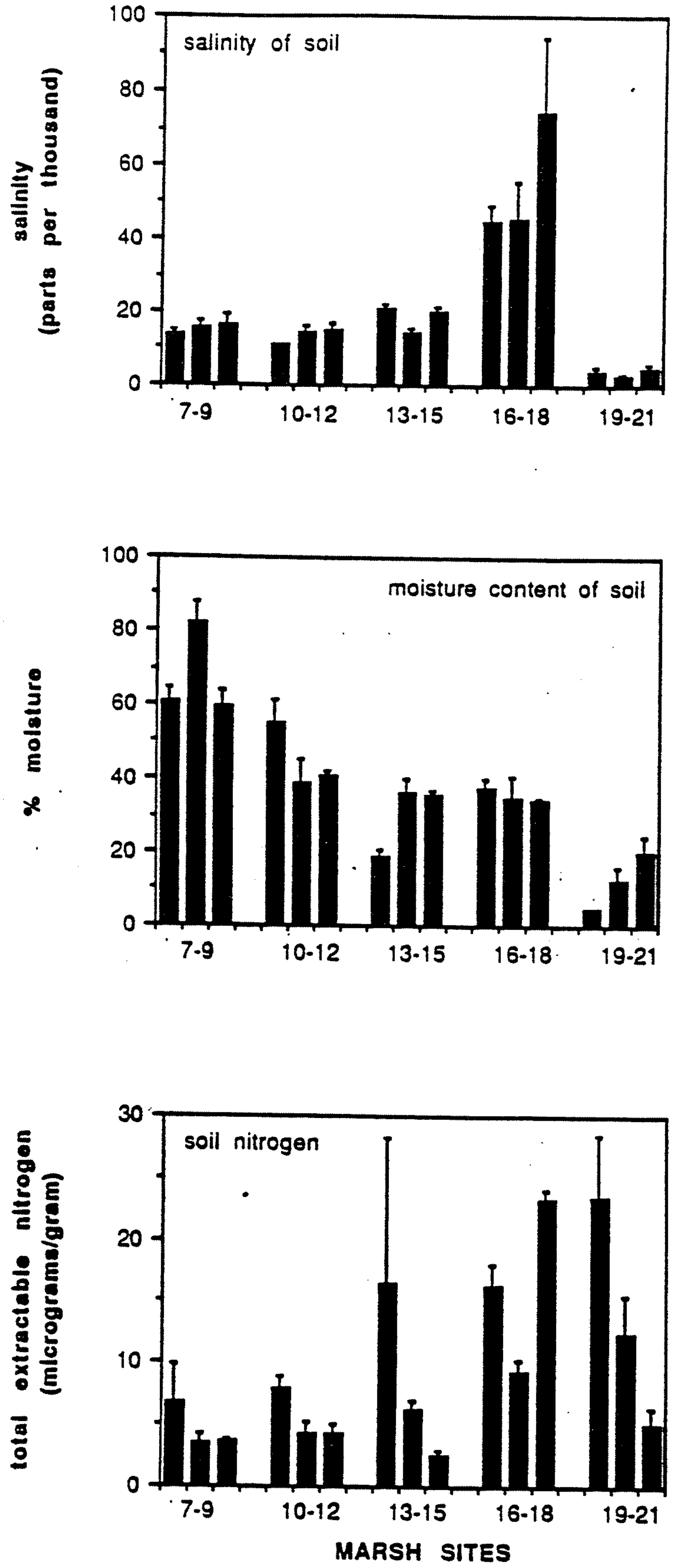


Figure 7. The salinity (A), the moisture content (B) and nitrogen content (C) of the soils at the marsh sites. The means of the three seasons (± 1 std. error) are given.

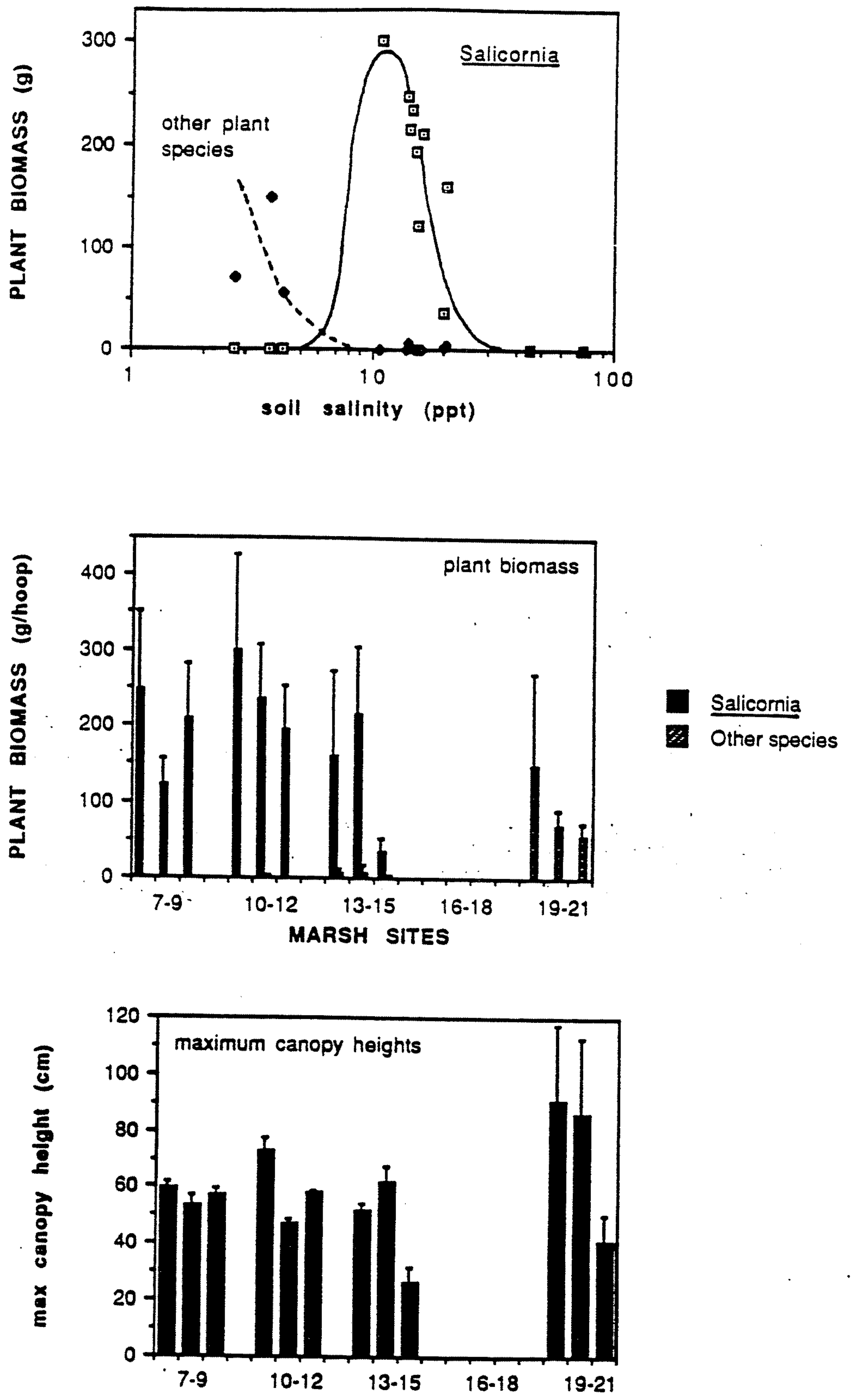


Figure 8. Plant biomass in the marsh sites as a function of soil salinity (A). The mean plant biomass in 1/10m^2 hoops (B) and the maximum canopy heights of the plants in the marsh sites (C); the means of the three seasons (± 1 std. error) are given .

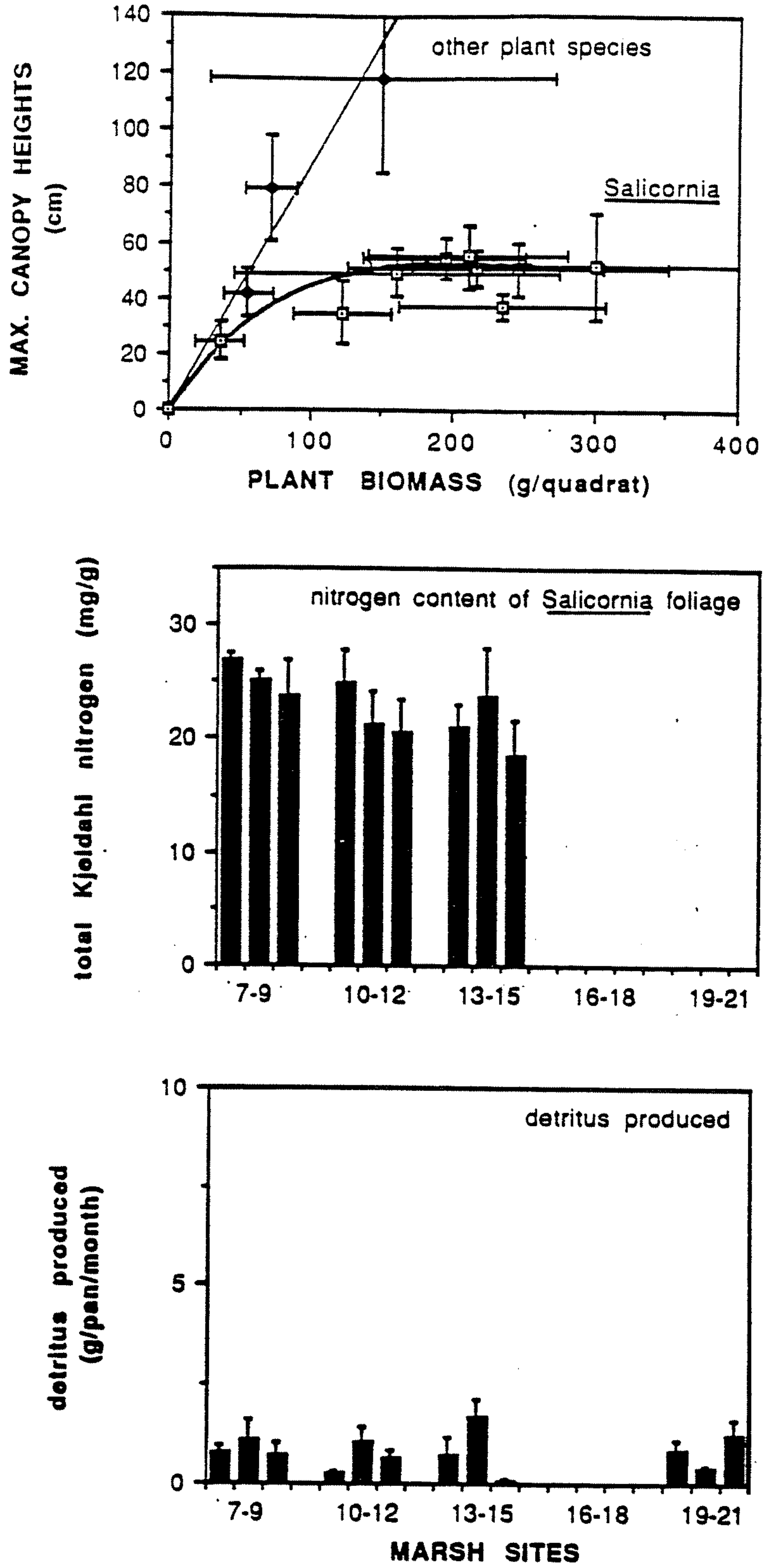


Figure 9. Maximum canopy heights as a function of plant biomass (A); the means of the three samples (± 1 std. deviation) are given for both factors. The nitrogen content of the *Salicornia* foliage (B) and the detritus produced at the marsh sites. The means of the three seasons (± 1 std. error) are given.

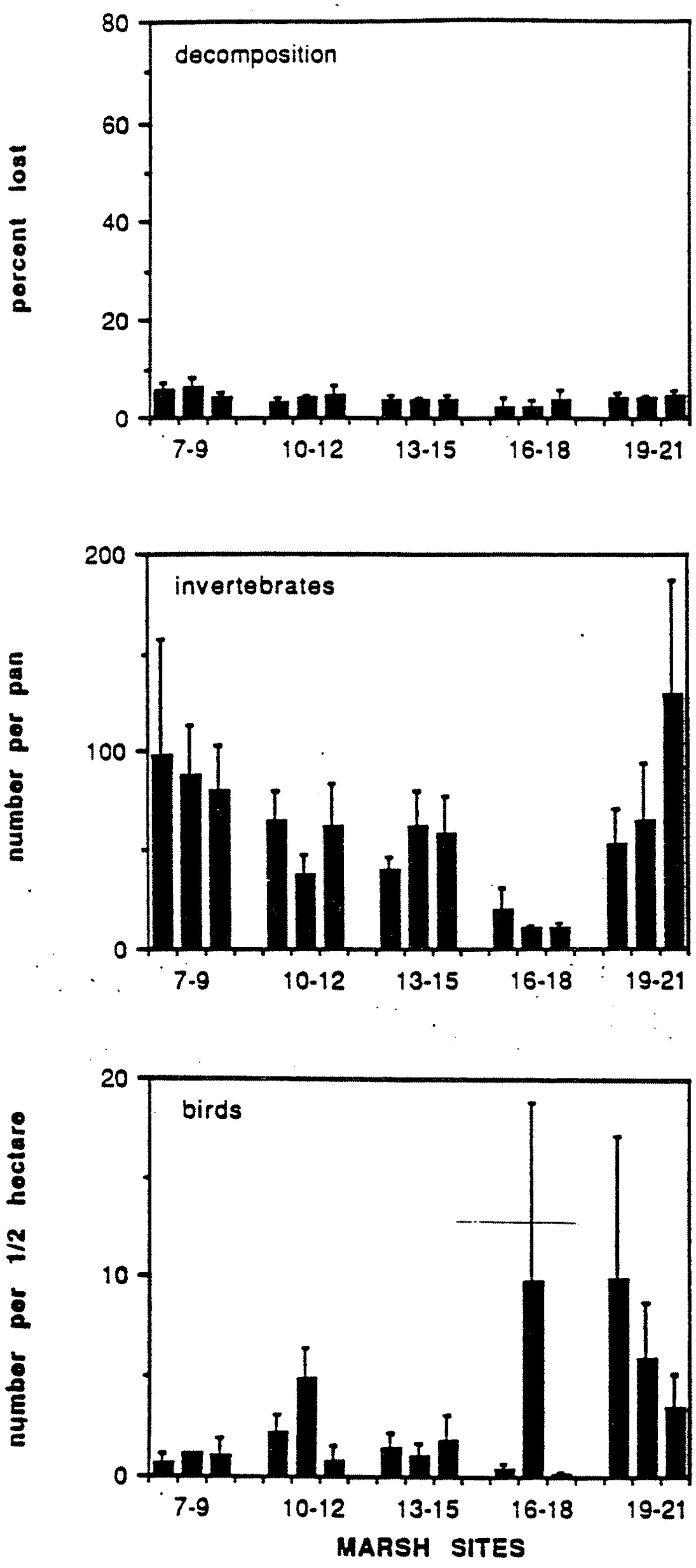


Figure 10. The decomposition rates (A), the abundances of invertebrates (B), and the abundances of birds in the marsh sites. The means of the three seasons (± 1 std. error) are given.

APPENDIX 1. The benthic invertebrates caught at the six Channel sites. The mean number of individuals per core ($n = 3$; core surface area = 78.54cm^2), is given. The results for the three seasons are presented separately in 1A, 1B and 1C.

APPENDIX 1A. Ballona Wetland benthic cores - April 1990

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
WORMS						
Spionidae - mean	7	1.3	3.7	0.3		
std d	8.2	1.5	6.4	0.6		
Capitellidae - mean	1.7	21.7	0.3	0.3		
std d	2.9	35.8	0.6	0.6		
Oligochaeta - mean	0.3	3.7				
std d	0.6	6.4				
Total worms	**9**	**26.7**	**4**	**0.7**	**0**	**0**
MOLLUSC						
Cerithidea californica - mean	4.7	8.3	0.7			
std d	4	10.4	0.6			
Macoma nasuta - mean		0.3				
std d		0.6				
Haminoea vesicula	X					
Total molluscs	**4.7**	**8.7**	**0.7**	**0**	**0**	**0**
CRUSTACEANS						
amphipods				X	X	
crab holes	X	X				
MISC						
Fish eggs - mean			4.7			
std d			8.1			
Total misc	**0**	**0**	**4.7**	**0**	**0**	**0**
TOTAL INVERTS (no misc) - mean	**13.7**	**38.7**	**4.7**	**0.7**	**0**	**0**
std d	**7.1**	**47.8**	**5.5**	**1.2**	**0**	**0**
std e	**4.1**	**27.6**	**2.7**	**0.4**	**0**	**0**
X = present in habitat but not in samples						

APPENDIX 1B. Ballona Wetland benthic cores - July 1990

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
WORMS						
Spionidae - mean	20.3	1.7	4			
std d	18.2	2.1	3.6			
Capitellidae - mean	9.7	1.7	0.7			
std d	9	2.9	1.2			
Oligochaeta - mean		3.3				
std d		3.3				
Total worms	30	6.7	4.7	0	0	0
MOLLUSC						
Cerithidea californica - mean	5.3	12.7	5.3	1.3		
std d	4	12.7	6.7	2.3		
Macoma nasuta - mean		0.3				
std d		0.6				
Assiminea - mean					0.7	
std d					1.2	
Total molluscs	5.3	13	5.3	1.3	0.7	0
CRUSTACEANS						
amphipods - mean			1.7			
std d			2.1			
crabs:						
Uta crenulata	X	X	X			
Pachygrapsus crassipes	X	X	X			
Total Crustaceans	0	0	1.7	0	0	0
TOTAL INVERTS - mean	35.3	19.7	11.7	1.3	0.7	0
std d	23	11.2	11.2	2.3	1.2	0
std e	0.6	6.4	6.5	1.3	0.7	0
X = present in habitat but not in samples						

APPENDIX 1C. Ballona Wetland benthic cores - October 1990

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
WORMS						
Spionidae - mean	2			2.3		
std d	2.6			3.2		
Capitellidae - mean	6.3	0.3		0.3		
std d	8.5	0.6		0.6		
Nereidae - mean	0.7					
std d	0.6					
Total worms	**9**	**0.3**	**0**	**2.6**	**0**	**0**
MOLLUSC						
Cerithidea californica - mean	3.7	8.7				
std d	3.2	5.7				
Tagelus californianus -mean		0.3				
std d		0.6				
Total molluscs	**4.7**	**9**	**0**	**0**	**0**	**0**
CRUSTACEANS						
amphipods - mean	0.3			0.3		
std d	0.6			0.6		
crabs:						
Uta crenulata		X				
Total crustaceans	**0.3**	**0**	**0**	**0.3**	**0**	**0**
TOTAL INVERTS - mean	**13.3**	**9.3**	**0**	**3**	**0**	**0**
std d	**12.7**	**4.9**	**0**	**3.6**	**0**	**0**
std e	**7.4**	**2.8**	**0**	**2.1**	**0**	**0**
X = present in habitat but not in samples						

APPENDIX 2. The nekton caught at the six Channel sites. The number of individuals per 10m of channel, is given. The results for the three seasons are presented separately in 2A, 2B and 2C.

APPENDIX 2A. Ballona Wetland nekton (number per 10m of channel) - April 1990

NAME				NUMBER	per 10m		
		Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
FISH							
Atherinops affinis	topsmelt		77				
Gillichthys mirabilis	longjaw mudsucker	2	13				
Acanthogobius flavimanus	yellowfin goby			X			
Clevelandia ios	arrow goby						
Fundulus parvipinnis	California killifish			X			
Gambusia affinis	mosquito fish			X	6	63	4
Leptocottus armatus	staghorn sculpin						
Total fish		**2**	**90**	**0**	**6**	**63**	**4**
INSECTS							
Corixidae	water boatmen	577		87			
Hydrophilidae	water scavenger beetles			11		10	2
Total insects		**577**	**0**	**98**	**0**	**10**	**2**
CRUSTACEANS							
crayfish							85
Total crustaceans		**0**	**0**	**0**	**0**	**0**	**85**
TOTAL NEKTON		**579**	**90**	**98**	**6**	**73**	**91**
X = present in habitat but not in sample							

APPENDIX 2B. Ballona Wetland nekton (number per 10m of channel) - July 1990

NAME				NUMBER	per 10m		
		Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
FISH							
Atherinops affinis	topsmelt						
Gillichthys mirabilis	longjaw mudsucker						
Acanthogobius flavimanus	yellowfin goby						
Clevelandia ios	arrow goby	8					
Fundulus parvipinnis	California killifish			X			
Gambusia affinis	mosquito fish			75	67	215	
Leptocottus armatus	staghorn sculpin						
Total fish		8	0	75	67	215	0
INSECTS							
Corixidae	water boatmen	600					
Hydrophilidae	water scavenger beetles					31	
Total insects		600	0	0	0	31	0
CRUSTACEANS							
crayfish							
Total crustaceans		0	0	0	0	0	0
TOTAL NEKTON		608	0	75	67	246	0

X = present in habitat but not in sample

APPENDIX 2C. Ballona Wetland nekton (number per 10m of channel) -October 1990

NAME				NUMBER	per 10m		
		Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
FISH							
Atherinops affinis	topsmelt						
Gillichthys mirabilis	longjaw mudsucker			1			
Acanthogobius flavimanus	yellowfin goby						
Clevelandia ios	arrow goby						
Fundulus parvipinnis	California killifish	3	3				
Gambusia affinis	mosquito fish	22	1	55	34	52	167
Leptocottus armatus	staghorn sculpin						
Total fish		**25**	**4**	**56**	**34**	**52**	**167**
INSECTS							
Corixidae	water boatmen	17		6			
Hydrophilidae	water scavenger beetles					7	
Total insects		**17**	**0**	**6**	**0**	**7**	**0**
CRUSTACEANS							
crayfish							135
Total crustaceans		**0**	**0**	**0**	**0**	**0**	**135**
TOTAL NEKTON		**42**	**4**	**62**	**34**	**59**	**302**

X = present in habitat but not in sample

APPENDIX 3. The birds seen at the six Channel sites. The numbers given are number of individuals per 200m of channel averaged over the three monthly censuses per season. The results for the three seasons are given separately in 3A, 3B and 3C.

APPENDIX 3A. Channel birds - Spring 1990

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
Great Egret		0.3	0.3			
Black-crowned Night Heron	0.7	0.3				
Mallard					0.7	
Killdeer			0.7			
Willet	0.3					
Red-winged Blackbird						1.0
Song Sparrow						X
Total individuals (sum of means)	1.0	0.6	1.0	0.0	0.7	1.0
Total species	2	2	2	0	1	1

X = seen in habitat but not in counts

APPENDIX 3B. Channel birds - Summer 1990

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
Great Blue Heron		1.3				
Green Heron	0.3			0.7		
Black-crowned Night Heron		1	0.3	0.3		
Spotted Sandpiper			X			
Wilson's Phalarope	0.3					
Belted Kingfisher						X
Mockingbird						X
House Finch						X
Song Sparrow						0.7
Total individuals (sum of means)	0.6	2.3	0.3	1.0	0.0	0.7
Total species	2	2	2	2	0	4
X = seen in habitat but not in counts						

APPENDIX 3C. Channel birds - Fall 1990

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
Great Egret	X					
Snowy Egret		X				
Great Blue Heron		X				
Green Heron		X		X		0.7
Blue-winged Teal	0.7	0.7				
Coot	X		0.3			
Black-bellied Plover		X				
Least Sandpiper		X				
Willet		0.3	0.3			
Belted Kingfisher	X	X				
Long-billed Marsh Wren						0.3
House Finch						1.3
Song Sparrow						0.7
Savannah Sparrow						0.3
Total individuals (sum of means)	0.7	1.0	0.6	0.0	0.0	3.3
Total species	4	8	2	1	0	5
X = seen in habitat but not in counts						

APPENDIX 4. The number of invertebrates, primarily insects, caught in pans at the "Marsh" sites. The numbers given are the mean number of individuals caught per pan averaged over three pans per site and three sites per habitat. The results for the three seasons are given separately in 4A, 4B and 4C.

APPENDIX 4A. Ballona Welland "insects" - April 1990

Sites:	# 7 - 9	# 10 - 12	# 13 - 15	# 16 - 18	# 19 - 21
CRUSTACEANS					
AMPHIPODS	11.5	0.1	0.0	0.0	0.0
ISOPODS	0.0	0.0	0.0	0.0	0.5
ARACHNIDS					
MITES	0.1	1.4	1.3	0.0	2.6
SPIDERS	11.8	2.7	2.8	0.4	10.0
INSECTS					
COLEOPTERA	1.2	1.6	4.1	0.1	2.6
COLLEMBOLA	19.4	4.6	28.6	0.6	102.4
DERMAPTERA	0.0	0.0	0.0	0.0	2.8
DIPTERA	43.9	31.2	12.7	4.0	23.5
HEMIPTERA	0.0	0.0	0.0	0.0	0.0
HOMOPTERA	18.9	14.4	11.1	1.6	4.5
HYMENOPTERA - ants	1.9	4.9	1.7	0.0	0.5
" - wasps	6.0	6.1	7.9	0.4	1.4
LEPIDOPTERA - adults	0.6	0.7	8.0	0.3	0.5
" - larvae	0.4	0.0	0.1	0.0	0.3
NEUROPTERA	0.0	0.0	0.0	0.2	0.0
ORTHOPTERA	0.0	0.6	0.0	0.0	0.7
THYSANOPTERA	1.9	1.5	1.3	0.4	0.8
unidentified insects	3.9	5.1	3.3	0.1	1.4
TOTAL	104.9	70.9	78.2	7.3	145.5

APPENDIX 4B. Ballona Wetland "insects" - July 1990

Sites:	# 7 - 9	# 10 - 12	# 13 - 15	# 16 - 18	# 19 - 21
CRUSTACEANS					
AMPHIPODS	32.2	0.5	0.0	0.0	0.0
ISOPODS	0.2	0.2	1.7	0.0	0.0
ARACHNIDS					
MITES	0.0	0.2	0.2	0.3	0.0
SPIDERS	1.3	3.3	2.0	0.3	4.7
INSECTS					
COLEOPTERA	1.0	1.7	1.7	0.2	2.8
COLLEMBOLA	5.0	2.5	3.3	1.3	0.7
DERMAPTERA	0.0	0.2	1.0	0.0	0.8
DIPTERA	23.7	15.0	21.3	5.0	2.5
HEMIPTERA	0.2	0.3	0.3	0.0	0.0
HOMOPTERA	3.8	6.0	2.5	1.2	3.7
HYMENOPTERA - ants	2.7	1.7	3.2	1.0	1.0
" - wasps	7.8	4.0	10.3	1.0	5.3
LEPIDOPTERA - adults	0.2	0.2	1.2	0.0	14.7
" - larvae	0.4	0.2	0.0	0.0	0.5
NEUROPTERA	0.0	0.0	0.0	0.2	0.0
ORTHOPTERA	0.2	0.5	0.2	0.0	0.2
PSCOPTERA	1.3	0.8	2.7	0.3	0.7
THYSANOPTERA	1.0	1.0	0.5	0.2	1.5
THYSANURA	0.0	2.5	0.8	0.2	3.7
unidentified insects	0.0	0.0	0.0	0.0	0.0
TOTAL	81.0	40.8	52.9	11.2	42.8

APPENDIX 4C. Ballona Wetland "insects" - October 1990

Sites:	# 7 - 9	# 10 - 12	# 13 - 15	# 16 - 18	# 19 - 21
CRUSTACEANS					
AMPHIPODS	8.5	0.0	0.0	0.0	0.0
ISOPODS	0.0	0.1	0.0	0.0	1.0
ARACHNIDS					
MITES	0.0	0.3	0.0	0.0	0.0
SPIDERS	1.0	0.8	1.0	0.7	0.3
INSECTS					
COLEOPTERA	0.0	0.3	0.8	0.0	2.8
COLLEMBOLA	9.7	10.4	5.3	0.4	23.9
DERMAPTERA	0.0	0.0	0.0	0.0	0.1
DIPTERA	6.5	12.3	2.2	2.3	3.8
HEMIPTERA	0.0	0.6	0.0	2.1	1.1
HOMOPTERA	3.8	4.9	6.6	1.4	6.4
HYMENOPTERA - ants	0.7	4.0	1.9	0.4	1.3
" - wasps	0.7	1.7	5.2	0.1	7.0
LEPIDOPTERA - adults	0.0	0.3	0.4	0.1	0.0
" - larvae	0.2	0.1	0.0	0.0	0.0
NEUROPTERA	0.2	0.4	0.0	0.4	0.2
ORTHOPTERA	0.0	0.0	0.0	0.0	0.0
PSCOPTERA	1.8	1.4	2.1	0.2	0.9
THYSANOPTERA	1.3	1.9	1.6	0.1	1.4
THYSANURA	0.0	1.9	1.2	0.1	2.1
unidentified insects	0.0	0.1	0.0	0.0	0.0
TOTAL	34.4	41.5	28.3	8.3	52.3

APPENDIX 5. The birds seen at the fifteen "Marsh" sites. The numbers given are number of individuals per 1/2 hectare averaged over the three monthly censuses per season. The results for the three seasons are given separately in 5A, 5B and 5C.

APPENDIX 5A. Marsh birds - Spring 1990

Sites:	# 7	# 8	# 9	# 10	# 11	# 12	# 13	# 14	# 15	# 16	# 17	# 18	# 19	# 20	# 21
Osprey				X											
Red-tailed Hawk							X								
American Kestrel										X					
Killdeer								X				0.3			
Willet	X														
Common Snipe					0.3										
Mourning Dove				X				X					X		X
Allen's Hummingbird							X								
White-throated Swift								X	X						X
Vaux's Swift	X			X											
Barn Swallow	X			X				X	X						
Violet-green Swallow															X
Cliff Swallow	X			X				X	X						X
Common Raven			X									0.3			
Western Kingbird				X					X						
Mockingbird				X				X							
Loggerhead Shrike			X						X			X			
Red-winged Blackbird									X						
Starling						X									X
Long-billed Marsh Wren							0.3	0.3							
Western Meadowlark	X		X	0.7					X		0.3		1.3	0.7	0.3
Savannah Sparrow	X	1.0	0.3	1.7	4.7		0.7	0.3	1.0	0.7	X				3.3
White-crowned Sparrow													8.3	10.0	1.0
House Finch		X													14.7
Total individuals (sum of means)	0.0	1.0	0.3	2.4	4.7	0.0	1.0	0.6	1.0	0.7	0.3	0.3	9.6	10.7	19.3
Total species	6	2	4	9	2	1	4	8	8	2	2	3	3	2	9
X = seen in habitat but not in count															

APPENDIX 5B. Marsh birds - Summer 1990

Sites:	# 7	# 8	# 9	# 10	# 11	# 12	# 13	# 14	# 15	# 16	# 17	# 18	# 19	# 20	# 21
Great Blue Heron		X													
Red-tailed Hawk								X							
American Kestrel															X
Black-bellied Plover											28.0				
Mourning Dove													X		X
White-throated Swift									X						
Vaux's Swift									X						
Barn Swallow	X	X							X	X			X	X	X
Cliff Swallow		X	X	X					X						X
Mockingbird	X	X	X	X					X						
Loggerhead Shrike	X			X		X		X	X						X
Western Meadowlark				0.7		X									0.3
Savannah Sparrow	0.3	1.3			2.0		0.3								
House Finch													3.3	1.0	
Total individuals (sum of means)	0.3	1.3	0.0	0.7	2.0	0.0	0.3	0.0	0.0	0.0	28.0	0.0	3.3	1.0	0.3
Total species	4	5	2	4	1	2	1	2	6	1	1	0	3	2	6

X = seen in habitat but not in count

APPENDIX 5C. Marsh birds - Fall 1990

Sites:	# 7	# 8	# 9	# 10	# 11	# 12	# 13	# 14	# 15	# 16	# 17	# 18	# 19	# 20	# 21
Great Blue Heron		X			3.3					1.0	0.3				
Great Egret					1.7						0.7				
Red-tailed Hawk														X	
American Kestrel														X	
Killdeer										X					
Willet					0.3										
Great Horned Owl				0.3											
Mourning Dove														X	
Say's Phoebe		0.3			X	X									
Black Phoebe		X													
Yellow Warbler	0.3														
Yellow-rumped Warbler			2.3										0.7		
Wilson's Warbler								X							
Mockingbird			X												
Loggerhead Shrike	X		0.3				X								
Long-billed Marsh Wren	1.0			X											
Western Meadowlark		X	X	X		X		1.7	0.3				X	0.7	X
Savannah Sparrow	0.3	0.7	0.3	3.0	2.3	2.3	3.0	0.7	4.0				3.3	5.3	5.3
White-crowned Sparrow													X	0.3	
House Finch													X	X	X
Total individuals (sum of means)	1.6	1.0	2.9	3.3	2.3	2.3	3.0	2.4	4.3	0.0	0.0	0.0	4.0	6.3	5.3
Total species	4	5	5	4	5	3	2	3	2	2	2	0	5	7	3

X = seen in habitat but not in count

APPENDIX 6. Red Fox abundances. The number and location of Red Foxes seen during our monthly bird censuses.

Month	Number	Location
March	1	Site 5
April	8	Sites 10, 11 (5 individuals), 12, 14
May	4	Sites 11, 13, 14, 20
June	1	Site 13
July	1	Site 16
August	2	Sites 10, 21
September	1	Site 11
October	0	-
November	2	Site 5 (2 individuals)