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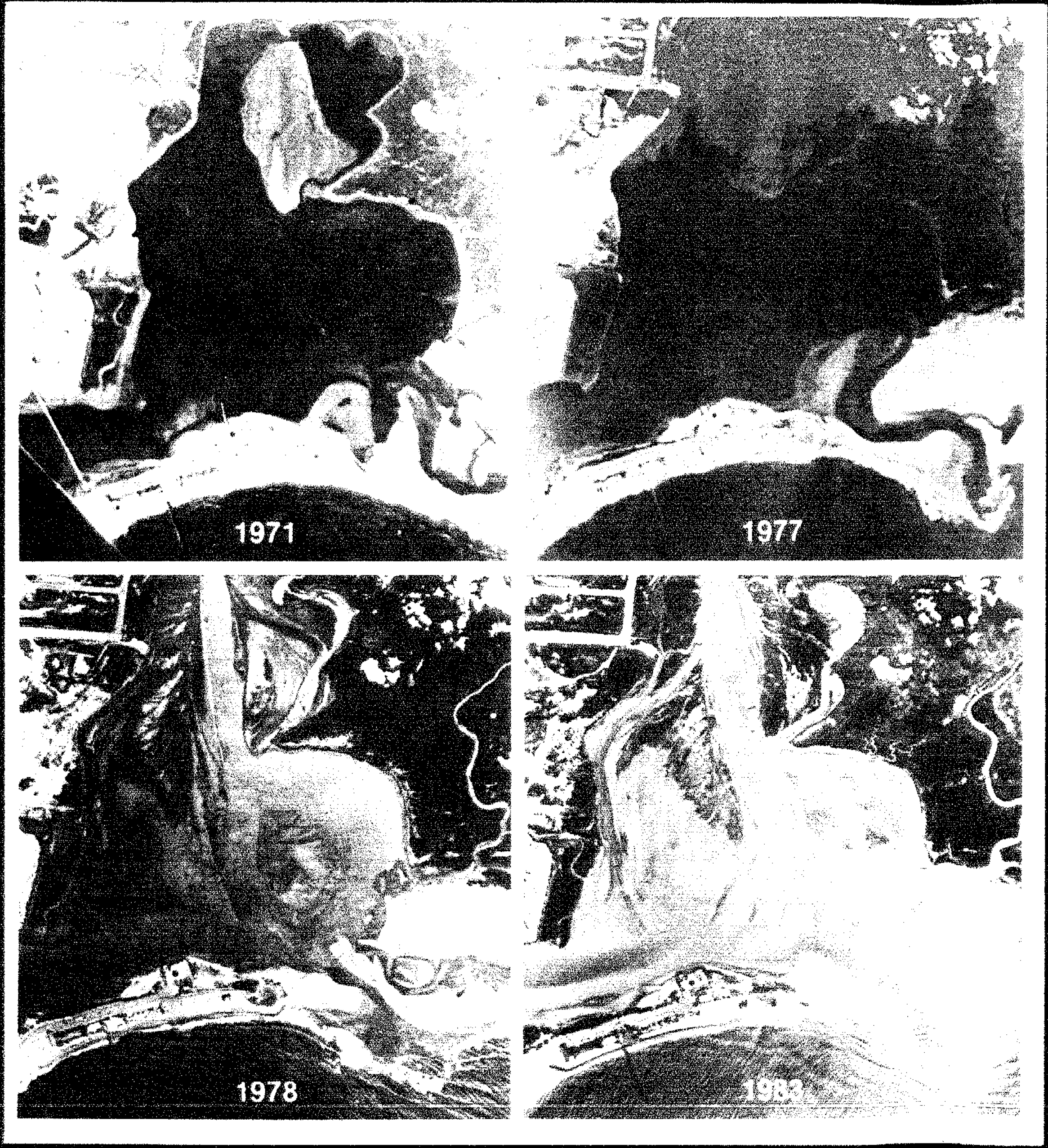
THE ECOLOGY OF MUGU LAGOON, CALIFORNIA:
An Estuarine Profile



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Cover photos:

Changes due to sedimentation in the central basin of Mugu Lagoon from 1971 to 1983.

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THE ECOLOGY OF MUGU LAGOON, CALIFORNIA: AN ESTUARINE PROFILE

by

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PREFACE

Mugu Lagoon is a tiny estuary. In any other coastal region of the United States, it would have attracted little attention. However, among the protected shallow-water embayments of the arid and steep Pacific Southwest, Mugu Lagoon is large, important, and relatively little disturbed (because of protection by the U.S. Navy for more than 40 years). Consequently, the lagoon has received considerable attention over the last 20 years, including intensive research on aspects of its geology and biology.

Over this same period, an awareness grew of how meager and in what jeopardy were the remaining estuarine resources of the region. With this growing awareness of the need to protect, manage, and enhance the remnants, the need to understand the functioning of these ecosystems became apparent. Accordingly, the endowment of scientific information on Mugu Lagoon became valuable for management.

This report is a synthesis of information on Mugu Lagoon, supplemented by other sources as necessary to provide an integrated treatment of ecosystem structure and function (Chapters 1-5). Although the analysis is most directly relevant to Mugu Lagoon, the rationale for much of the research and especially for this synthesis was that the characterization of this relatively healthy system would serve as a model and yardstick for application to other, usually more highly modified coastal wetland ecosystems in the region. Comparisons between the well-functioning standard and other systems of concern should reveal malfunction and suggest remedies (Chapter 6).

Unfortunately, events of the last decade have altered the "health" and little-disturbed state of the Mugu Lagoon ecosystem. Sedimentation caused by major storms virtually eliminated the largest open-water area of the lagoon and completely altered the bottom characteristics of another major section of the lagoon. Protection of the lagoon, its fringing marshes, and adjacent uplands were ineffectual in shielding the system from inputs originating in the farther reaches of the watershed.

This report chronicles how the impacts of those alterations ramified through the estuarine ecosystem. In retrospect, this case history of startling and profound alterations occurring so suddenly may be more instructive for management of the region's embayments and their associated wetlands than the original objective of using Mugu Lagoon as the "pristine" standard for guiding management. Chapter 7 presents some of these management considerations.

The information base for this synthesis is weak in some topical areas where that for the companion report in this series, "The Ecology of Tijuana Estuary: An Estuarine Profile" by Joy Zedler, is strong. Reference to that source is encouraged, particularly regarding the analysis of factors influencing primary productivity and salt marsh community structure.

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CONVERSION TABLE

Metric to U.S. Customary

Multiply	By	To Obtain
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
meters (m)	0.5468	fathoms
kilometers (km)	0.6214	statute miles
kilometers (km)	0.5396	nautical miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters (m^3)	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons (t)	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees (°C)	1.8(°C) + 32	Fahrenheit degrees

U.S. Customary to Metric

inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
statute miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
square miles (mi^2)	2.590	square kilometers
acres	0.4047	hectares
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	283.5	milligrams
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
pounds (lb)	.00045	metric tons
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees (°F)	0.5556 (°F - 32)	Celsius degrees

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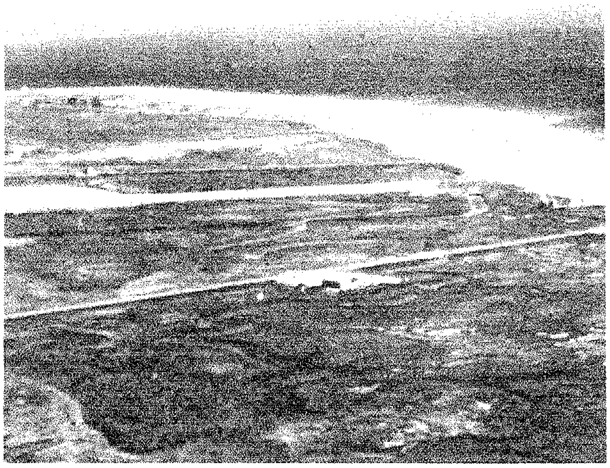
ACKNOWLEDGMENTS

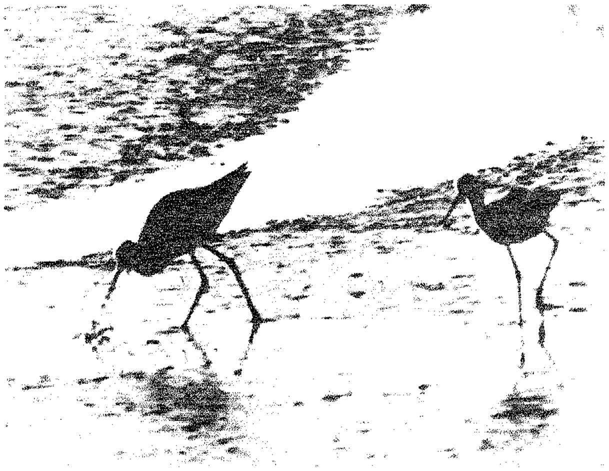
I am grateful to the many people whose help made this monograph possible. My first debt of gratitude is to my colleagues Bob Holmes and Pete Peterson for getting me started in Mugu Lagoon. My second debt of gratitude is to my two principal coworkers, Millicent Quammen and Gary Shaffer, whose unstinting efforts and close cooperation helped me learn most of what I know about Mugu Lagoon. Most of our studies were only possible because of the assistance of many students in the field and laboratory.

I benefited from close contact with Joy Zedler, Wayne Ferren, and Eric Metz for a broader perspective on southern California coastal wetlands. Much of the research on which this synthesis relies was supported by the California Sea Grant College Program. I thank the Commander, U.S. Naval Air Station, Point Mugu, for the opportunity to conduct research in Mugu Lagoon and Base Biologist Ron Dow for his cooperation. I also benefited from the outstanding human and material resources of the Library, University of California, Santa Barbara, especially Government Publications and the Map and Imagery Laboratory. The comments of technical reviewers, including Keith Macdonald, Pete Peterson, and Joy Zedler, helped me improve the report and I thank them. Reviews by the U.S. Fish and Wildlife Service Field Office, Laguna Niguel, California, and the Natural Resources Management Office at Naval Air Station, Point Mugu, helped eliminate errors. June Phinney typed and retyped the manuscript speedily, cheerfully, and well, for which I thank her. Penny Herring, Sue Lauritzen, Kate Lyster, and Rob Brown of the National Wetlands Research Center expertly assisted with production. Without the assistance of Ed Pendleton as reviewer, arbiter, and emissary of goodwill under trying circumstances, there would be no report.

I dedicate the report to Millicent Quammen, where her indispensable contributions are not acknowledged by authorship, and Nathaniel Onuf, for the time stolen from him to complete this large task.

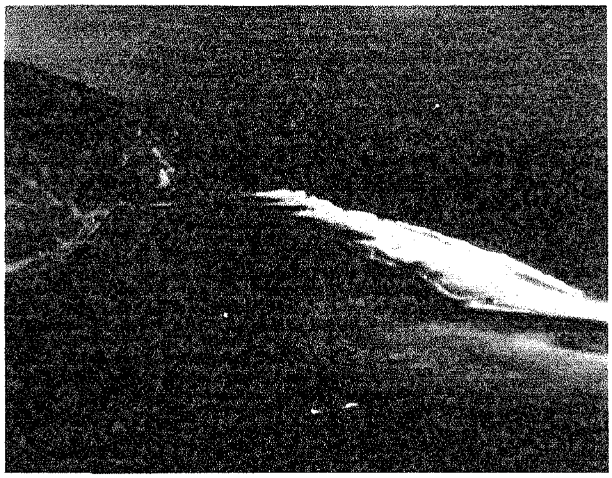


West tidal creeks, looking east, at Mugu Lagoon (photo by R. Dow).

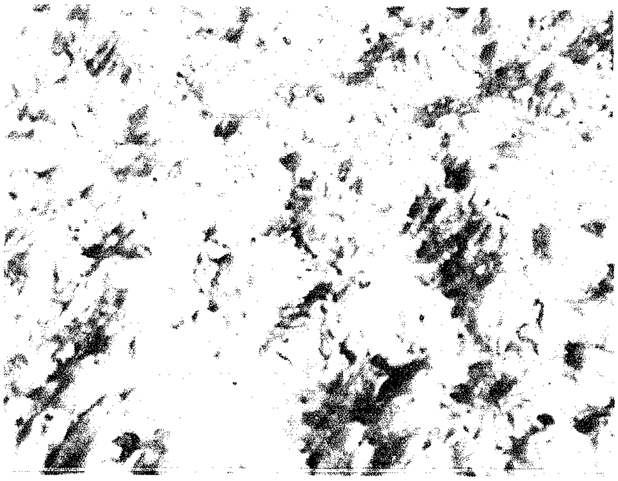


Mudflats with foraging shorebirds (photo by Millicent Quammen).

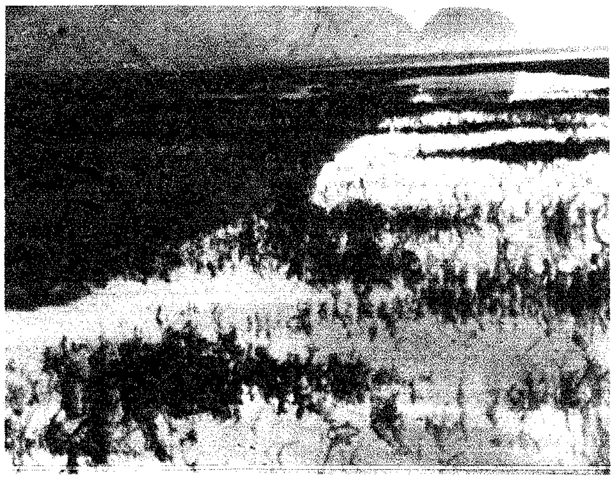
Central Basin of Mugu Lagoon (photo by R. Dow).



Central and east arms of Mugu Lagoon (photo by R. Dow).



East Arm, low tide, burrows of Callianassa californiensis (photo by R. Dow).



East arm of Mugu Lagoon at high tide (photo by R. Dow).

CHAPTER 1. INTRODUCTION: HISTORICAL PERSPECTIVE AND OVERVIEW

Estuaries are not estuaries most of the time in the Pacific Southwest of the United States. The little rain that falls is confined to one-half of the year, during which the average monthly evaporation exceeds average monthly precipitation in all months at coastal points (U.S. Environmental Data and Information Service 1980).

When the effects of transpiration of water back into the atmosphere by the vegetation are included, the deficit in near-surface water is magnified. In addition, the watersheds are small and steep, but the mountains that delimit them landward are not high enough to retain snow for long. Consequently, little water concentrates or is stored at or near the surface. Therefore, coastal streams and even rivers are intermittent or seasonal, as are the flows into coastal embayments.

Human activities have tended to further reduce the amount and duration of freshwater inputs. Natural waterways are circumvented by damming, distributing the waters to human dwellings, recollecting those waters, now laden with wastes, and dumping them directly into the ocean. Because the burgeoning human population has encroached into natural floodways, southern California has become "the land of the paved river" to insure that surface water does not tarry long where it might damage manmade structures. The net result is that little becomes less and even more limited in duration. Hence, my assertion that these estuaries are not estuaries most of the time, follows Donald Pritchard's introductory definition in the American Association for the Advancement of Science (AAAS) symposium volume Estuaries, published in 1967: "An estuary is a semi-enclosed coastal body of water which has a free connection with the open sea and within which seawater is measurably diluted with freshwater derived from land drainage."

In the land of estuaries that are not estuaries most of the time, perhaps it is altogether fitting that the first subject for an estuarine profile was not an estuary in any sense until 1884, when it became so by the hand of man (Steffen 1982). Echoing Joy Zedler's often repeated theme in her community profile on "The Ecology of Southern California Coastal Salt Marshes," no aspect of the functioning or present character of this region's estuaries can be pursued very far without reckoning with the effects of past, present and future human activities, both within and surrounding the embayments.

One other characteristic of these intermittent estuaries of the Pacific Southwest interacts with the just-mentioned features of climate and recent history to set these wetland ecosystems apart from their counterparts in other coastal regions of the United States. Because the coast has been uplifted so recently, it is steep. As a result, these areas of shallow coastal water protected from the violent wave action of the open coast are few, small, and separated from one another by long stretches of very different shore environments--usually narrow sand or rock platform beaches backed by cliffs.

In net, estuaries, intermittent or otherwise, have been historically rare in the region. Rapid development by humans has made these environments even rarer and has degraded many surviving areas. Nevertheless, as elsewhere, the combination of protection from violent wave action, shallow water, ample sunlight (even to the bottom of subtidal areas), regular tidal exchange, and equable climate yield an abundant and varied biotic environment. Not surprisingly, some organisms have come to depend on these productive coastal areas: as necessary stopping places and overwintering areas for several migratory bird species that use the Pacific Flyway, possibly as the only nursery ground for at least one commercially important fish stock (see Chapter 5), and as the only habitat for three species now classified as endangered. Thus, rarity is a major ingredient of the significance of coastal wetlands in southern California (Onuf et al. 1979), and concern about continuing losses and degradation is urgent.

Urgent concern, coupled with the several distinctive characteristics shared among southwestern intermittent estuaries but distinguishing them from the estuaries of the other regions, prompted the compilation of an estuarine profile for southern California. Mugu Lagoon was chosen for a variety of reasons, of which I list three. Among the few, in some cases forlorn, remaining wetlands in southern California, Mugu Lagoon is noteworthy for its (1) relatively large size and (2) its freedom from many of the human incursions that afflict other areas (because the lagoon and its surrounding salt marsh lie within the fenced and patrolled boundary of a military reservation). Consequently, there was some reason to believe that a wide range of coastal wetland habitats was represented at Mugu Lagoon in natural relations to one another; i.e., Mugu Lagoon provided a glimpse of what these systems could be like when free of undue human intervention. Perhaps, then, Mugu Lagoon could serve as a model for undoing damage to other wetlands. This was my reason for conducting research in Mugu Lagoon. The security provided by the Navy also was an inducement to carry out long-term observations and experiments that could not have been contemplated where access was not strictly controlled. As a result, (3) more detailed scientific research has been performed at Mugu Lagoon than any other coastal wetland area in southern California, although coverage of different topics is very uneven.

1.1 GEOLOGIC HISTORY

There must be an element of arbitrariness in the decision of when to begin the history of a place, particularly for one such as Mugu Lagoon, perched on the edge of an actively moving continental plate. Because of this precarious location, the region is incredibly active tectonically. What is here now bears little relation to even its recent antecedents.

The region is very active. The stream that empties into the lagoon originates in the wild jumble of the Transverse Ranges (oriented east-west or transverse to the north-south trend of the major ranges of California, the Sierra Nevada and the Coast Range) only 50 km from the San Andreas Fault (Figure 1). Along the fault, instantaneous rates of lateral displacement of 6.4 m and 3.0 m were identified with the San Francisco earthquake of 1906 and the Imperial Valley earthquake of 1940, respectively (Hill 1954). Within the Transverse Ranges, only 25 km from the boundary of the lagoon's watershed, a 0.9-m vertical displacement occurred along a thrust fault during the San Fernando earthquake of 1971. The estimated average rate of uplift along the thrust faults of the region is 8 m per 1,000 years (1 cm in 1.25 year). In some locations rates are bound to be much higher (Scott and Williams 1978). In summary, quoting from Scott and Williams: "Deposits of late Pleistocene age are in a steeply inclined attitude at many localities in the area, and are actually overturned at several - to within 50° of complete overturn in Orcutt Canyon, a study watershed. In fact, the structural deformation of deposits of the youngest geological time period in the Transverse Ranges is without known parallel in North America."

Even though very recent processes are almost exclusively responsible for the present physiographic character of the region, the kind of material exposed by tectonic processes and weathering also is important. It is the parent material of

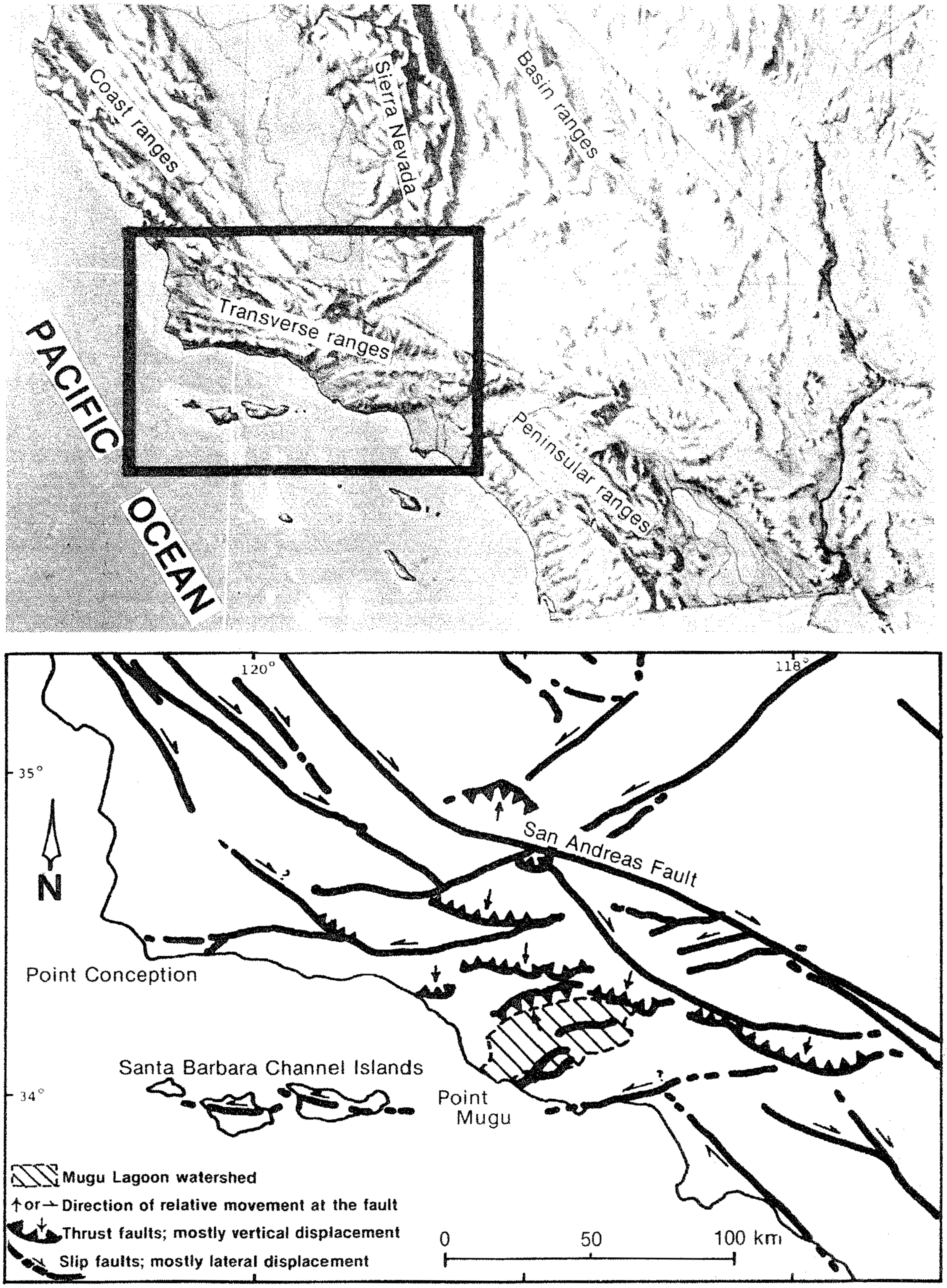


Figure 1. Major structural features of southern California. Upper relief map shows the relationship of the Transverse Ranges to the other major mountain ranges of southern California. Lower map shows the watershed of Mugu Lagoon in relation to major fault systems (adapted from Hill 1954).

the soils and influences their fertility and erodibility. Therefore, I begin the history of Mugu Lagoon in the Upper Cretaceous, approximately 100 million years ago, when the oldest rocks now exposed in the watershed were laid down. The location on an active continental margin is attested by the alternation of marine (deep, transgressive, and nearshore) and terrestrial deposits in the stratigraphic record (Table 1). All rocks are sedimentary, with the exception of one convulsion of volcanic activity in the Miocene. These volcanic rocks are exposed in the southeastern part of the watershed but apparently underlie more recent deposits everywhere else in the region, judging from samples extracted during well drilling (Shelton 1954). Parenthetically, it is the Miocene sedimentary deposits that have excited the greatest interest locally. They are considered to be the source rocks for petroleum reserves in the Ventura area (Steffen 1982).

According to Steffen's recent summary, the features that eventually defined the lagoon itself have been developing only in the last 300,000 years, since the Middle Pleistocene. Flood deposits from the Santa Clara River built up the Oxnard Plain at the rate of 2 m per century, until uplift at the end of the Middle Pleistocene directed the river to the northwest. At around the same time, the southeast portion of the plain subsided. Sea level reached its lowest stand about 18,000 years ago and then rose to 2 m above present levels approximately 3,000 years ago. This was when the lagoon first formed. Where littoral drift from the northwest (Bascom 1980) encountered the Point Mugu headland, sand accreted, and a much broader beach or spit formed on the upcurrent side of the obstruction. As the sea level dropped, the spit migrated seaward with it, and the enclosed coastal embayment has become the Mugu Lagoon Estuary.

Table 1. The alternation of marine and terrestrial formations in the stratigraphic sequence of the watershed of Mugu Lagoon. Adapted from Steffen (1982).

Years before present	Geological age	Depositional environment
	Cenozoic:	
600,000	Pleistocene	Terrestrial
10,000,000	Pliocene	Deep marine
25,000,000	Miocene	Transgressive marine[a]
35,000,000	Oligocene	Terrestrial
55,000,000	Eocene	Nearshore marine
65,000,000	Paleocene	Nearshore marine
	Mesozoic:	
100,000,000	Upper Cretaceous	Terrestrial

[a] Coarse particles deposited in shallow water and fine particles in deep water.

Evidence for this process has come from Warme (1971), who identified ridges of sand within the salt marsh that fringes the eastern arm of Mugu Lagoon. He interpreted the ridges as relict beach berms that had formed during a higher stand of the sea. Apparently, the drop in sea level was stepwise rather than continuous. If it had been continuous, it would be hard to account for the water-filled trough (the lagoon) that lies between the current and past berms, rather than dunes or a wall of sand such as climbs the flank of the headland 5 km to the southeast.

1.2 RECENT HISTORY

Mugu Lagoon has a water area of approximately 130 ha. Judging from the distribution of recent lagoonal deposits overlying deltaic deposits, it was ten times that size at its largest (Figure 2). Presumably, this was soon after the origin of the lagoon when the sea level was 2 m higher. The lagoon is elongate, running parallel to the coast for 5.6 km but never exceeding 1 km transversely. It is composed of two long arms projecting out from a broader central basin. Calleguas Creek, the only inlet stream, discharges into the central basin. The mouth of the lagoon usually opens in the vicinity of the central basin, but it has been known to migrate 0.75 km eastward. The eastern

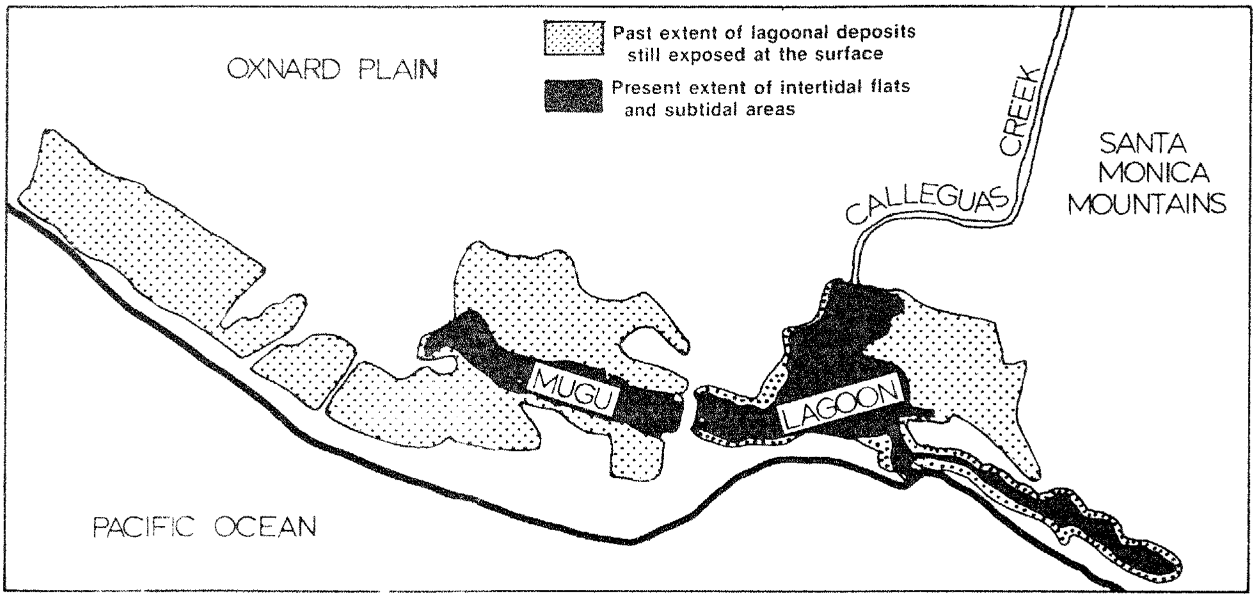


Figure 2. Extent of Mugu Lagoon sediments (from Steffen 1982, based on a geologic map in California Division of Mines and Geology, Preliminary Report 14, 1973).

arm is very narrow because the shore is steep along the flank of the Santa Monica Mountains. The western arm is broader and has a wider expanse of fringing salt marsh, because in this direction the lagoon extends into the Oxnard Plain.

Human occupation of the area around Mugu Lagoon probably began around 7,000 years ago (Macdonald 1976a). The coastal strip along the Santa Barbara Channel supported one of the densest aboriginal populations in what is now the United States--which is surprising, considering that the California Indians were hunter-gatherers and not agriculturalists (Hornbeck 1983). The Chumash village on Mugu Lagoon at the time of European contact (1760) was estimated to have 400 inhabitants, but densities dropped off rapidly inland (Hornbeck 1983). The high local density of hunter-gatherers indicates that the Indians could have had a large effect on populations of fishes and the larger invertebrates in Mugu Lagoon and game in the surrounding uplands, while effects on the watershed would be minimal. During the period of the Spanish missions and Spanish and Mexican ranchos (1782 to 1846), agriculture was introduced. Although mission records show that substantial amounts of wheat were harvested in the Ventura area (Hornbeck 1983), the main agricultural activity in the watershed of Mugu Lagoon was grazing cattle (Murphy 1979). Presumably, some changes in the natural vegetation resulted, but the character of the landscape probably did not change.

Soon after Mexican control was supplanted in the region (1846), "Anglo" settlers began to intensively cultivate large areas of the watershed of Mugu Lagoon. Between 1876 and 1881 railroad connections with San Francisco and the eastern United States were established, and agriculture became a big export business (Steffen 1982). Shortly after crop agriculture became established on the Oxnard Plain, Calleguas Creek was channelized, and its flows were shunted into the lagoon. As already indicated, Mugu Lagoon has been a true lagoon rather than an estuary for most of its existence. In 1884 Mugu Lagoon became an estuary.

Before the channelization of the creek, there were no significant terrigenous inputs to the lagoon. Conditions probably approximated those of a coastal marine embayment. Undoubtedly, large areas of the Oxnard Plain contiguous to the lagoon were freshwater marshes during the rainy season, but their flows into the lagoon would have been small compared to that of a channelized Calleguas Creek. The original watershed of the Santa Monica Mountains draining into the lagoon was little more than twice the water area of the lagoon itself and less than the area of the lagoon plus its fringing salt marsh. Consequently, interactions with the ocean, sunlight, and temperature would have been the physical driving forces rather than freshwater inflow. The tidal prism (volume of lagoon water exchanged over a tidal cycle) would have been sufficient to keep the mouth open at all times. Regular tidal flushing coupled with shallow depths would have assured good exchange of materials within the lagoon; however, the mouth of the lagoon is at the head of a submarine canyon, and the Continental Shelf is narrow in any case. Therefore, the water entering the lagoon often is relatively nutrient-poor, oceanic-blue water. In the absence of terrestrial runoff, this may have resulted in lower primary production than is characteristic of most shallow-water marine systems. Nevertheless, the combination of shallow water protected from violent wave action, ample sunlight, higher summer water temperatures than offshore, and good tidal exchange must have made for an abundant and productive biota (as is attested by the shell middens on the shore of the lagoon).

The major human influence on Mugu Lagoon has been the funneling of discharges from a watershed of 843 km^2 into a receiving body less than 1/500th that size, which previously had been subject only to marine influences. The repercussions of that single alteration will be touched on throughout the rest of this report. Although the alteration was a single discrete event, its effect can grow, and almost certainly has grown. The channelized creek is a conduit. It will transmit whatever is put in along its length to its lower end. As more people occupy the watershed or use it more intensively, the inputs to the creek will be altered. In 1880, 4 years before Mugu Lagoon became an estuary, the population of Ventura County was 5,073. The population has more than doubled in every 20-year period since then and in 1980 was 529,174, or more than 100 times greater than a century ago. Between 1970 and 1980 the population within the watershed increased by 56% from 154,465 to 240,432.

The cause and effect relationship between the number of people and the amount of material that has potential impact if it is carried into an estuary is not straightforward. For instance, population growth in this region could have the beneficial effect of increased diversion of water to pathways that do not lead into the estuary. Instead, the effect of greater significance is as follows: The bottomlands have been under cultivation for a long time. The growth of the population in this area takes the form of urbanization of these bottomlands. If the process were strictly the substitution of a different land use on the same spot, the net result might well be less input to the natural drainage system. However, displacement rather than substitution has occurred. Rather than being eliminated, intensive agriculture has moved up the sides of steep hills, there substituting groves of fruit trees with bare soil between the trees for grazed chaparral. This type of cultivation increases runoff, possibly with substantial loads of agricultural chemicals, and aggravates soil erosion.

Another consequence of the preemption of prime agricultural bottomlands is that the large remaining acreage is farmed even more intensively. The average frost-free period is 332 days. Customarily, three to four crops are grown each year in the Oxnard Plain area (Steffen 1982), and some of them are heavily dosed with chemicals. The strawberry fields, for instance, are covered with plastic so that the soil can be fumigated for nematodes, weed seed, and fungi before each planting. An average of 193.1 lb per acre (213.9 kg per ha) of restricted fumigant pesticides (almost exclusively methyl bromide and chlorpicrin) is applied each year. In 1976, almost 800,000 lb (360,000 kg) of pesticides were applied in Ventura County (California Department of Food and Agriculture 1978), the great majority within the watershed of Mugu Lagoon. Although figures for fertilizers or, more importantly, levels of pesticide residues or nutrients in agricultural drain waters are few, the potential for substantial inputs to Calleguas Creek and Mugu Lagoon obviously is high.

Not all effects of development by humans are transmitted to the lagoon via its inlet stream. The lagoon lies within the boundaries of the U.S. Naval Air Station at Point Mugu, California, (established in 1946), and the operational part of the base is built on fill dredged from the central basin. Past activities within the lagoon itself, especially those associated with the construction of the base, have led to large losses of wetland habitat and other modifications that have altered ecosystem function. However, natural resources incontestably benefit from the military presence in other regards. The relatively large part of Mugu Lagoon that remains a wetland has been left as natural as possible, given the modifications of its surroundings. The protection began as a byproduct of naval security and air clearance space requirements but now is an actively pursued policy of the Navy. As a result, the site has been something of a mecca for scientific study for many years.

The current situation and probable near-term trends, then, are these: The watershed is dominated by agriculture; however, a burgeoning urban-suburban population has led to changes in agricultural practices that almost certainly increase the inputs of sediments and chemicals to the lagoon. The limited availability of freshwater locally and the probable increase in water conservation and wastewater reclamation may well reduce future inputs of stream water and what it carries during most of the year, but storm flows still will deliver sediments to the lagoon, sometimes in great gluts. The consequences of this sedimentation will be explored at length in other sections of this report.

So far in this overview of Mugu Lagoon, the "estuary" has been treated as a unit--initially a very small one, essentially without a watershed, and now a much bigger one, with concomitantly larger terrigenous inputs. Every effort will be made to encompass the whole system; however, there are major constraints. Inevitably, coverage is uneven. Some topics (most notably associated with the shelled invertebrates) have been well studied, while others (most glaringly, nutrient chemistry) have not been investigated. Furthermore, almost all of the ecological research that has been carried out in Mugu Lagoon has been in the eastern arm of the lagoon, which is maintained by the Navy as an ecological reserve. This limitation in spatial coverage should be borne in mind throughout. Whenever appropriate, the discussion will be extended to include the other parts of the lagoon.

CHAPTER 2. ENVIRONMENTAL SETTING

Generally speaking, average conditions provide the most informative and most often utilized summary of what a system is like and how it is likely to behave. However, it will become abundantly obvious that extreme conditions play a role in Mugu Lagoon that is vastly more important than their frequency would suggest. The main thrust of this section will be, then, to illustrate how important departures from average conditions are in determining the characteristics of this estuary and probably most others in the region. Later chapters will show how the terrestrial part of this estuarine ecosystem exerts its influence over the estuary through the supply of sediments. Therefore, many of the topics of this chapter will be developed as they relate later to the production or transport of sediments to the lagoon.

2.1 REGIONAL GEOLOGY AND CHARACTERIZATION OF THE WATERSHED

The watershed around Mugu Lagoon is notable for its high erosion potential. Erosion is a leveling process. It is the predominating force in determining the surface characteristics of most land masses. Slopes are determined primarily by the rates of weathering of the parent rocks and the length of time that erosion has been working on them. As erosion proceeds, slopes become more gradual, thereby slowing the rate of subsequent erosion. However, in parts of the Transverse Ranges of California, including much of the watershed of Mugu Lagoon, this is not the case. The rates of uplift substantially exceed the rates of denudation. The great tectonic activity that now prevails, and has prevailed for at least the last 100 million years, has produced a very youthful landscape. About 46% of the watershed is covered by late Pleistocene or more recent alluvial deposits (Figure 3). These dominate the flat valley bottoms. The older rocks have been thrust up along faults and folded into ranges of hills and mountains. Elevations are moderate (under 1,200 m), but slopes are considerably steeper than they would be in the absence of ongoing uplift. Thus, past erosion has not yielded a reduction in slope that lessens present erosion, and the measured rates of denudation "approach the maximum for areas in which consolidated bedrock is being eroded directly" (Scott and Williams 1978). Scott and Williams also stated that the failure of standard models to include this factor of tectonic activity accounts for their gross underestimates of sediment yield in this region.

The mineral composition and structure of the rocks in this region also contribute to very high sediment yields. The divisions of rock types in Figure 3 were made to correspond to the categories used by Andre and Anderson (1961) in their tests of soil erodibility with respect to parent material. According to their preferred index of erodibility (surface-aggregation ratio), soils from Quaternary alluvium and acid igneous rocks were the most erodible soils that they tested. These soils cover 59% of the watershed. The Miocene volcanics and Quaternary alluvium and terrace deposits of the Transverse Ranges were approximately twice as erodible as the consolidated sedimentary rocks (Scott and Williams 1978); however, this factor was minor compared to the effect of tectonic activity on erosion.

The juxtaposition of active mountain building next to a coastal plain has produced soils ranging from a thin veneer to more than 1.5 m deep. Soils range from

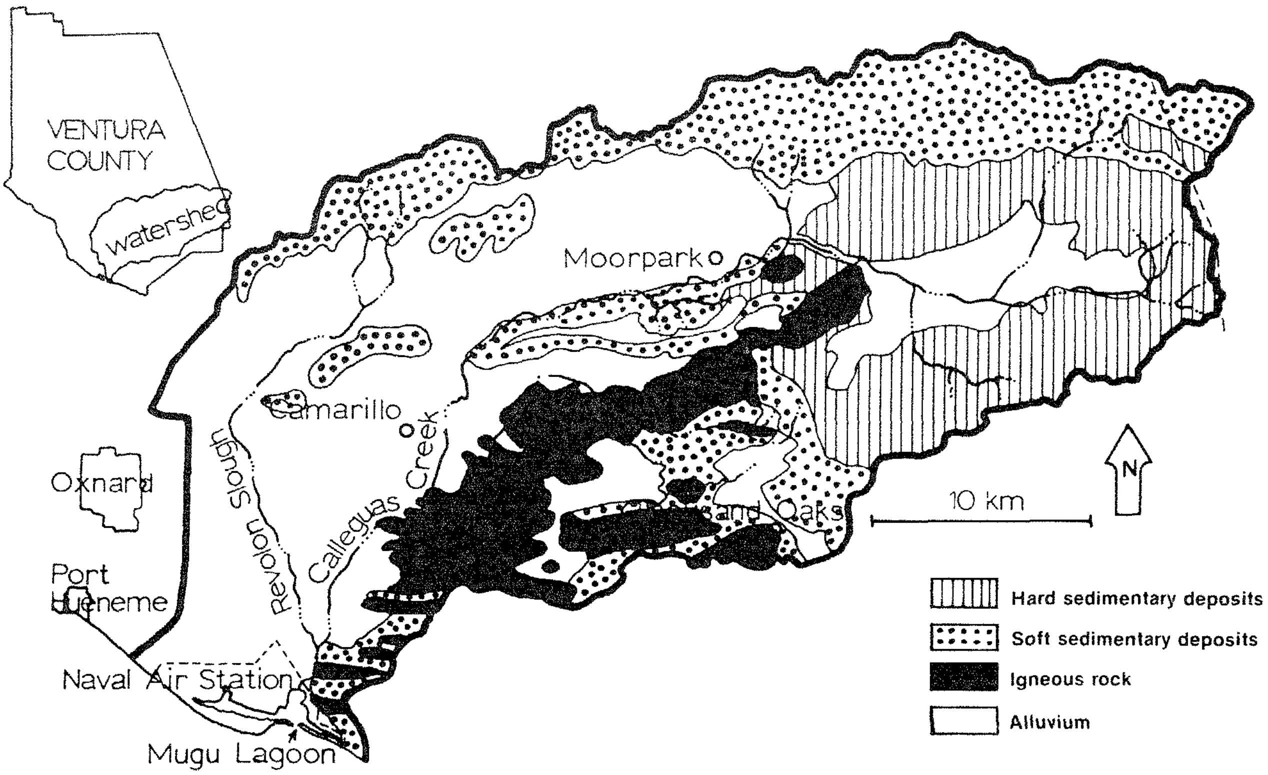


Figure 3. Geological map of the watershed of Mugu Lagoon. Within the watershed, rocks are grouped according to the categories of Andre and Anderson (1961): hard sedimentary deposits (Cretaceous, Paleocene, and Eocene marine shale, sandstone, and conglomerate, and nonmarine Oligocene); soft sedimentary deposits (Miocene, Pliocene, and lower Pleistocene marine deposits); igneous rocks of Miocene age; and alluvium (Quaternary alluvial and terrace deposits, mainly nonmarine). (Adapted from Jahns 1954.)

prime agricultural land to land completely unsuitable for cultivation, with use restricted to the maintenance of wildlife and watershed, according to the Soil Conservation Service's capability classification. As one might expect from the discussion of geological factors, the thin soils that are unsuitable for agriculture invariably are associated with steep slopes, and the prime soils are all in the valley bottoms (Figure 4a).

Coastal sage and foothill woodland with islands of oak savanna are the dominant natural communities (Figure 4b). They are not closely linked to soil type or capability class. Agricultural uses of the watershed (Figure 4c) are dominated by vegetable crops on prime agricultural land of the coastal plain; fruit/nut crops in the lower reaches of the valleys, both on prime bottomland and marginal valley sides; field crops in the upper reaches of valleys, mostly on soils with severe limitations for cultivation; and grazing in the rugged hills. Nursery operations are interspersed throughout the vegetable and fruit/nut growing areas. Soils of high fertility are interspersed in most soil types and capability classes (California Department of Food and Agriculture 1978). Apparently, in this region of obligatory irrigation, factors other than fertility determine the suitability of a soil for agriculture.

The effect of vegetative cover and land use on erosion is well known in principle but less well known in actual application to this region. Throughout the watershed the natural vegetation can be sparse and

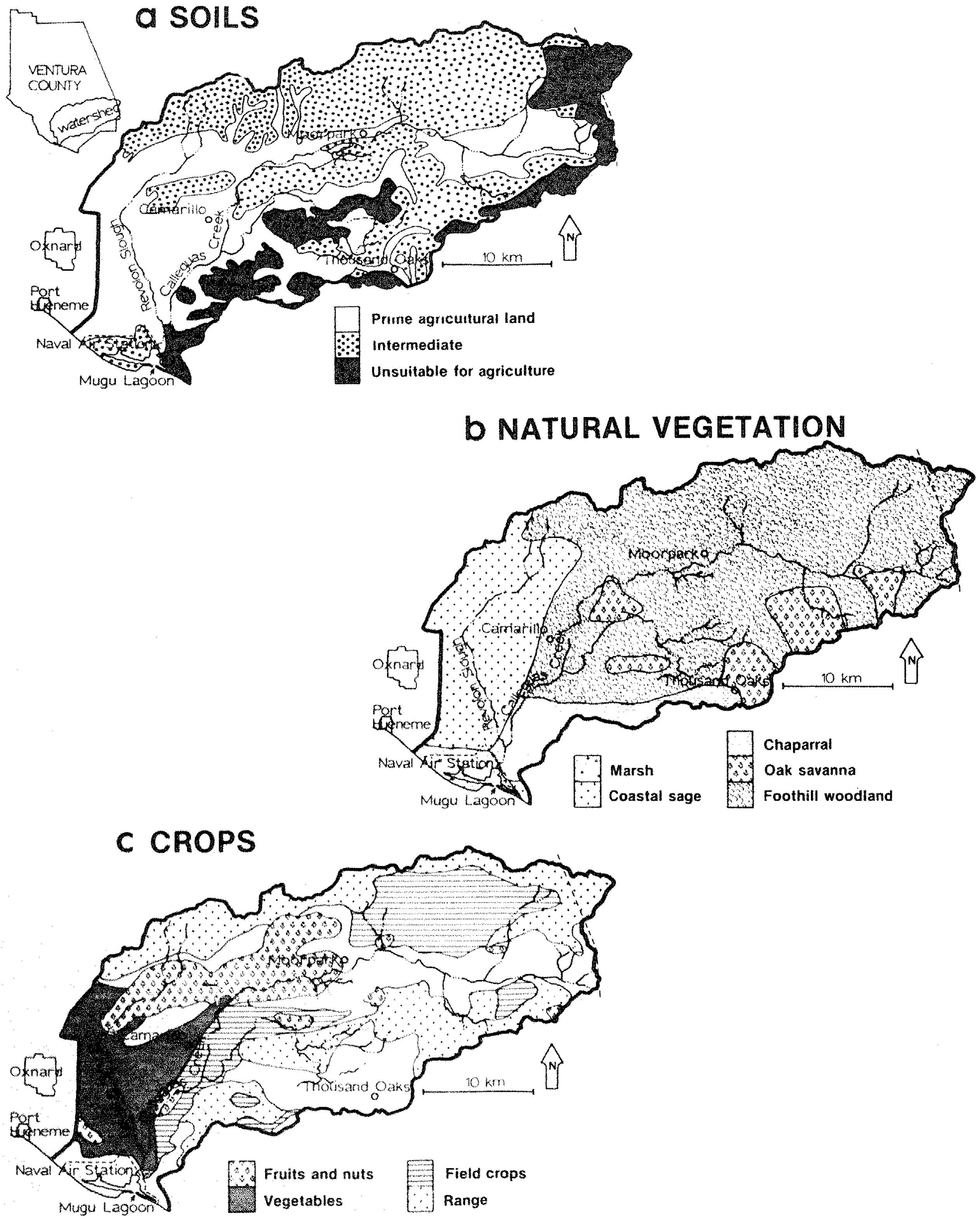


Figure 4. Characteristics of the Mugu Lagoon watershed: (a) suitability of soils for agriculture, (b) natural vegetation, and (c) agricultural crops (adapted from California Department of Food and Agriculture 1978).

slopes can be precipitous; therefore, the thousands-fold differences in soil loss shown in early Soil Conservation Service tests between plots of similar area and slope with natural vegetation compared to planted and bare crop land probably do not apply to these areas. Nevertheless, the effect of land clearing on erosion is very large. For instance, measurements of sediment yield in the western Transverse Ranges of Ventura County were 11.9 to 35 times higher immediately after the total burn of watersheds than after 10 years of regrowth (Scott and Williams 1978). The effects of agriculture have not been addressed explicitly in the context of local conditions; however, Steffen (1982) mapped areas of high erosion rates (greater than 10 tons per acre per year or 20 metric tons per ha per year) and estimated that accelerated erosion (caused by human activities) contributes about 40% of the total sediment generated in the watershed. Almost all of the accelerated erosion is associated with agriculture.

2.2 CLIMATE

The climate of the area is Mediterranean: moderate temperatures, arid summers, and relatively moist winters. The reason for the region's moderate temperature regime is the Pacific Ocean, a highly conservative thermal mass over which westerly, onshore winds prevail except from November to January (de Violini 1975).

Monthly mean air temperatures of the warmest and coldest months (Figure 5a) differ by only +3.5°C and -3.1°C from the annual mean of 14.7°C. The mean daily range in temperature is least in June, varying 7.3°C from a minimum of 12.3°C to a maximum of 19.6°C, and greatest in November, varying 10.6°C from a minimum of 9.2°C to a maximum of 19.8°C, only 3.3°C more than in June. Even the minimum temperature recorded in 26 years is not particularly extreme (-2.8°C or 9.4°C below the average minimum of the coldest month; de Violini 1975). However, the high temperature discrepancies are greater. The record high was 40.0°C, 17.9°C higher than the average maximum of the warmest month. More importantly, from July 1976 through January 1981, temperatures were greater than 10°C above the average maximum of the warmest month more than 2 days per year, on the average. Curiously, these extremes were not during the height of summer (July and August). Rather, they were both before (May and June) and especially after (September, October, and even November).

During October and November, the hot spells are usually associated with very low relative humidities and high winds, the so-called Santa Anas, when the prevailing westerlies are supplanted for up to a few days at a time by northeasterly winds swooping down the canyons from the high desert--the air is hot to begin with and rises even more in temperature as the air mass descends and is compressed. The significance of the hot, dry winds at this time of year will be apparent following the discussion of precipitation.

Generally, the daily and seasonal temperature fluctuations tend to increase with distance from the ocean, and temperature decreases with elevation. Locally this pattern is strongly modified by the winds, because of the orientation of the watershed. Thus, most of the time the prevailing westerly winds transmit the moderating influence of the ocean throughout the coastal plain and up into the east-west trending valleys. Nevertheless, both higher maximum and lower minimum temperatures certainly occur in the more landward parts of the watershed than at Mugu Lagoon.

The other important characteristic of a Mediterranean climate is that the relatively small annual precipitation is heavily concentrated in the cooler part of the year. Certainly this is the case for Mugu Lagoon (Figure 5b). Ninety-six percent of the yearly total precipitation falls in the 6 months from November to April. The contrasting records for the years of lowest and highest precipitation are plotted along with the 34-year mean to give some idea of the extent of year-to-year variation (Figure 5b). Yearly totals were more than twice the 34-year average in 2 years, more than 1.5 times the average in 6 years, and less than

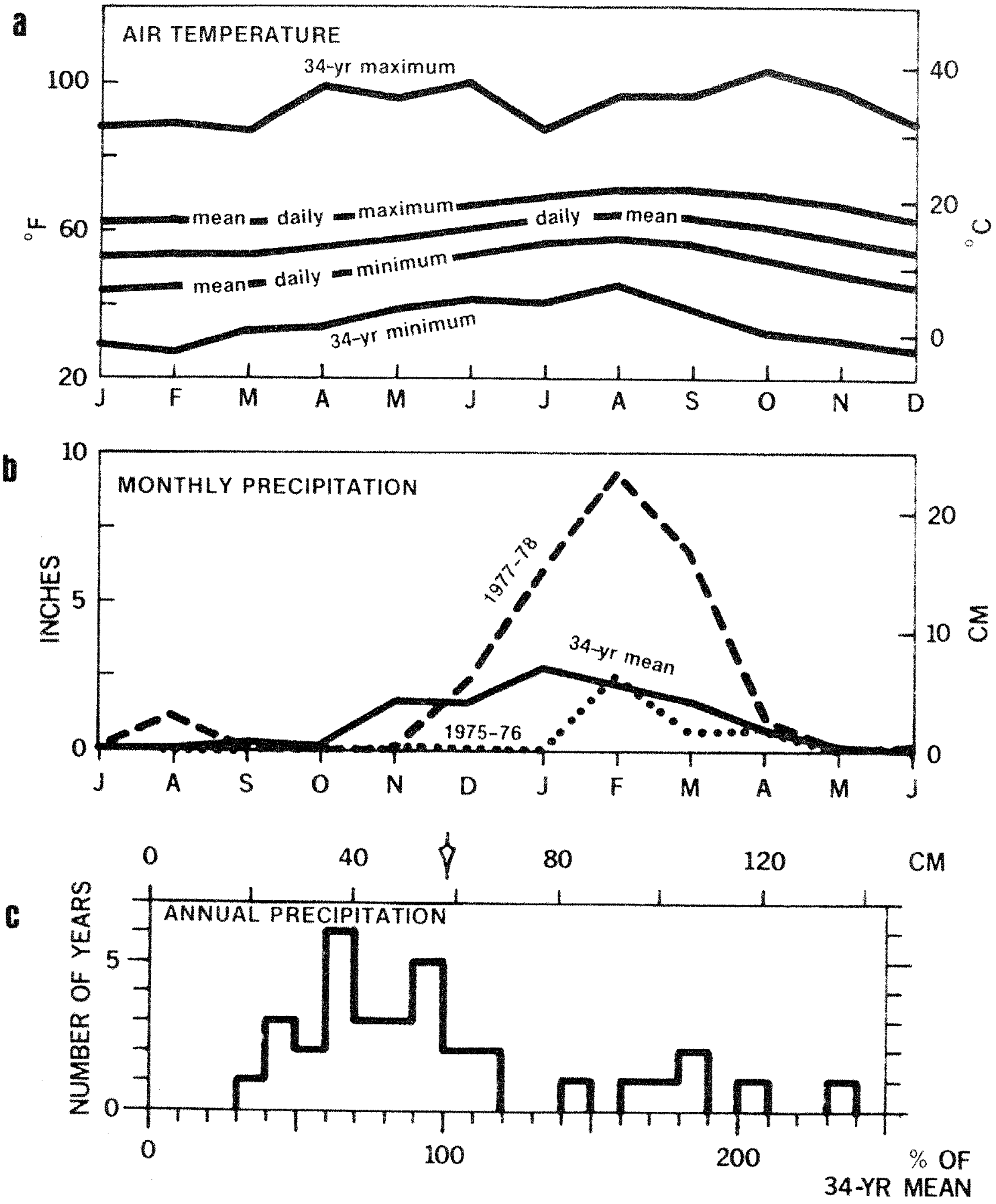


Figure 5. Characteristics of the climate of Mugu Lagoon: (a) air temperature, (b) monthly precipitation, and (c) the number of years with different amounts of precipitation, grouped in 10% increments of the 34-year mean (adapted from de Violini 1975 and unpublished records).

one-half the average in 4 years (Figure 5c). Rainfall is concentrated into short periods within the 6-month moist period. In 2 years out of 34, the average annual rainfall was exceeded by precipitation falling in a single month; in 9 years over one-half of the annual average fell in a single month (and in each of 2 months in 1978 and 1980 for a total of 11 occurrences). After these figures, it will come as no surprise that even a single storm, or more precisely a storm series, can dump more than the annual average (as, for example, in February 1962 and January 1969).

Both of these characteristics of the local rainfall regime (occurrence limited to the cool half of the year and then falling in a relatively few major storms) have serious implications in the watershed of Mugu Lagoon. Potential evapotranspiration is more than 70 cm during the growing season; yet, because water is rapidly removed from the surface layers of the soil, the estimated actual evapotranspiration is 25 - 30 cm. Since almost no rain falls after April, range grasses are likely to dry out by early June (Soil Conservation Service 1970), with the four hottest and four of the driest months yet to come. When the Santa Anas blow near the end of this period, the hot, dry, fast-moving air desiccates even the most deeply rooted vegetation.

Fires ignited under these conditions tend to burn out of control until the Santa Ana conditions abate. In the meantime, thousands of acres of vegetation can be consumed. Based on records for their study area in the western Transverse Ranges, which included substantial parts of the watershed of Mugu Lagoon, Scott and Williams (1978) cited annual burn rates of 0.42% of the total area, although longer records from the national forests immediately to the north indicate that a higher rate might be more appropriate. This suggests that an average of 2 km^2 of the rugged part of the watershed is bared by fire each year, with the previously described ten-fold or more magnification of sediment yield. Even in the absence of fire, the vegetation of the watershed is in very poor condition by the next rainy season. Undoubtedly this also contributes to the high sediment yields characteristic of the region.

The significance of the concentration of rainfall in major, protracted storms is given in Scott and Williams' (1978) description of the January 1969 event:

> "Major storms, like those of March 1938 and January and February 1969, have followed a generally similar pattern that can be expected to recur in future major storms. The storm of January 18-27, 1969, was typical: The circulation pattern of a low pressure center in the Pacific permitted intense streaming of northeastward moving, moisture-laden air as a succession of storm fronts. Precipitation was light until January 19 when intensity increased sharply. Heavy precipitation occurred throughout most of January 19-26, was interrupted by a brief respite on January 22, and then climaxed on January 25.
>
> "The January 1969 storm generally produced peak discharges equal to or greater than those of the 1938 storm in Ventura County and western Los Angeles County. The 1938 storm had been the greatest storm of recent times, at least since the legendary flood of 1862, and its peak discharges and sediment yields have been widely used as standards of flood magnitude and as criteria for impoundment structures....
>
> "In both the 1969 storm periods, surface saturation occurred well before the most intense precipitation. Similar antecedent conditions existed during the 1938 storm and can logically be assumed to recur during any future major storm."

Once soil is saturated, no matter what the soil type or cover is, all subsequent precipitation will run off. Consequently, the same intensity of rain will yield much greater peak runoffs after saturation than before. Although the relationship is anything but direct or precise, analyses made under local conditions suggest that sediment yield is a function of peak runoff flow to the 1.67 power (Scott and Williams 1978, citing Ferrell

1959). If so, a doubling in peak flow would be associated with more than a tripling in sediment yield. In extreme cases, soil saturation on steep slopes may result in slope failure and slumping, partly accounting for the extreme sediment input to places like Mugu Lagoon.

Steffen (1982) pointed out one additional feature of the timing of precipitation in this region that is inherently interesting and bears on this matter of sediment yield. Building on Troxell and Hofmann's (1954) interpretation of variations in tree-ring width as evidence of a long succession of alternating wet and dry periods from 1385 to the present in the Los Angeles region (Figure 6), Steffen suggested the high likelihood that major storms at the beginning of a wet sequence (median length 12 years during 1385 - 1954) would cause much more erosion. He based this conclusion on the observation that the condition of the vegetation would be worst at the end of a dry sequence (median length 15 years over the same time span) but would improve rapidly during a wet sequence, thereafter lessening the erosive impacts of storms.

2.3 HYDROLOGY

Runoff is rapid in the Mugu Lagoon watershed because so much of the watershed is steep, yet low enough in elevation that precipitation is not stored as snowpack. The rapid runoff, coupled with the concentration of rainfall into a few major storms usually separated by dry spells of a few to several weeks, means that there is little or no surface flow in the lower reaches of local streams except during and immediately after storms. Almost all freshwater inflow to Mugu Lagoon, therefore, occurs from November to April (Figures 5b and 7a); even within that winter period, most freshwater inflow is concentrated in a few pulses (Figure 7b). These gluts of freshwater during storms can carry vast amounts of suspended material that, in turn, can be deposited in the still waters of the lagoon. The concentration of freshwater inputs in rare but extreme

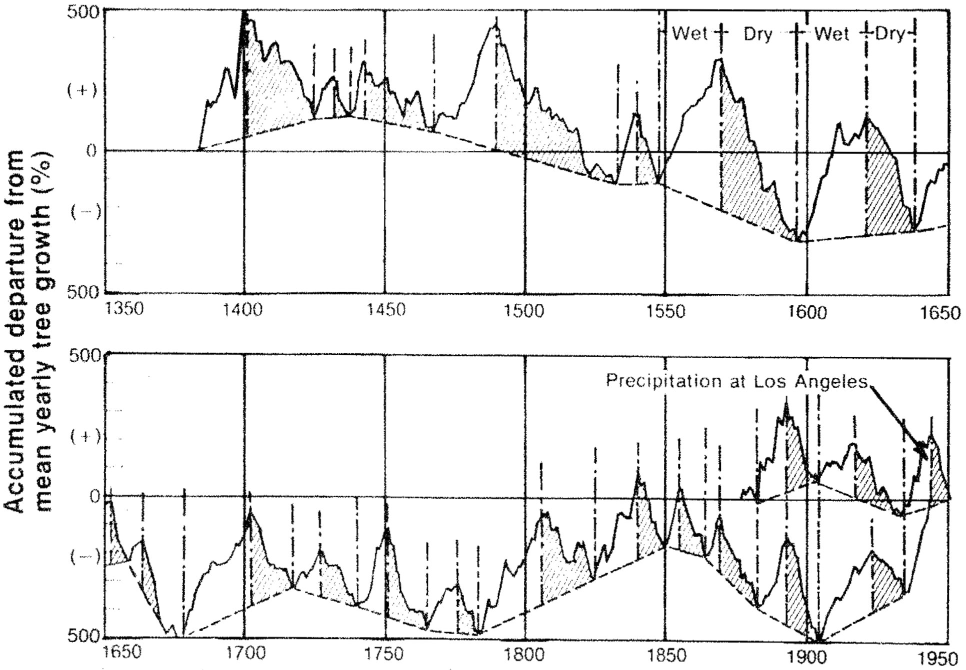


Figure 6. Wet and dry periods in southern California (from Troxell and Hofmann 1954).

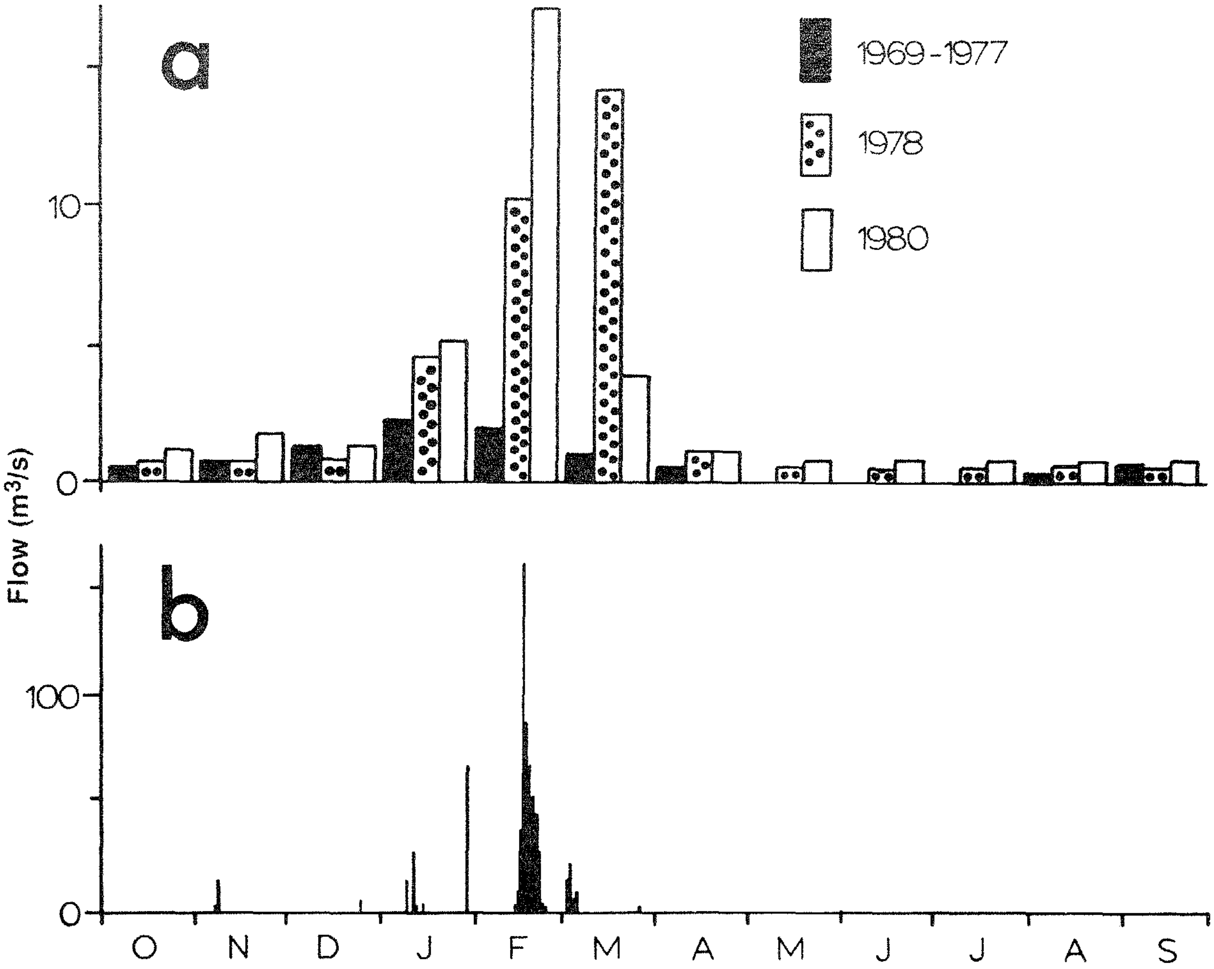


Figure 7. Streamflow in Calleguas Creek: (a) mean flow in different months 1969-77, 1978, and 1980; (b) mean flow by day in 1980 (from USGS records for the gauge at Camarillo State Hospital).

events is responsible for some striking effects which will be discussed after the biota has been introduced. Here, it will suffice to say that the freshwater input to Mugu Lagoon completely flushes the lagoon for short periods of time rather than creating a longitudinal salinity gradient that moves up or down the estuary as the freshwater input changes seasonally. During the remainder of the year, the lagoon is completely marine.

The preceding generalization is not applicable at the very mouth of Calleguas Creek. Agricultural irrigation and sewage plant return waters make for a continuous, small input of freshwater. Because much of this water comes directly from intensively cultivated lands, toxic substances and nutrients could affect water quality. Little information on this problem or this part of the lagoon is available (see Section 7.3).

Mugu Lagoon continues to be marine-dominated most of the time, even since it has become an estuary. The tides are responsible for the majority of day-to-day inputs and removals of materials. The tidal prism (volume of water moved in and out of the lagoon by the tides) is large compared to the volume retained at lowest water. Persistent southeast longshore currents prevail along the coast in this region. This assures that very little of the water departing the lagoon on the ebb tide is returned on the following flood tide; i.e., the same water mass is not under the influence of lagoonal conditions for long.

The tides themselves differ from one tide to the next (mixed semi-diurnal pattern characteristic of this coast), from week to week (spring-neap alternation), and from season to season (higher highs and lower lows in summer and winter than in spring and autumn). The maximum tidal range is 3 m. A sill at approximately mean sea level at the mouth of the lagoon eliminates changes in water level below mean sea level within the lagoon and reduces the maximum tidal range of the lagoon to 1.7 m above mean sea level (Figure 8). Consequently, on some neap tides the volume of water exchanged is negligible, whereas on spring tides it is more than three times the volume retained at low water, at least in the eastern arm (Onuf and Quammen 1983). Not only are upper intertidal areas submerged less of the time than lower intertidal areas, but also the interval between their submergences becomes increasingly variable. The lowest intertidal areas are submerged at least once a day, whereas at +1.5 m MLLW (Mean Lower Low Water, the long-term average elevation of the sea at the lower low tide each day,the standard tidal datum of the region), periods of consecutive daily submergence lasting 4 to 25 days are separated by 1- to 11-day periods without submergence. At +2.0 m MLLW, 2- to 7-day periods of consecutive daily submergence are separated by as few as 7 to as many as 56 days without submergence. There is little or no lag in the times of spring high tides between ocean and lagoon; however, there may be more than an hour's difference in the timing of high tides during other portions of the lunar cycle.

Because of the relatively large tidal exchange of water within the lagoon most of the time and the narrow opening to the sea, currents are fast near the mouth. Currents were measured at 3.7 km/h on a neap tide, and were estimated to be more than 10 km/h on spring tides (Warme 1971). The sill at the mouth has the effect of prolonging the ebb portion of

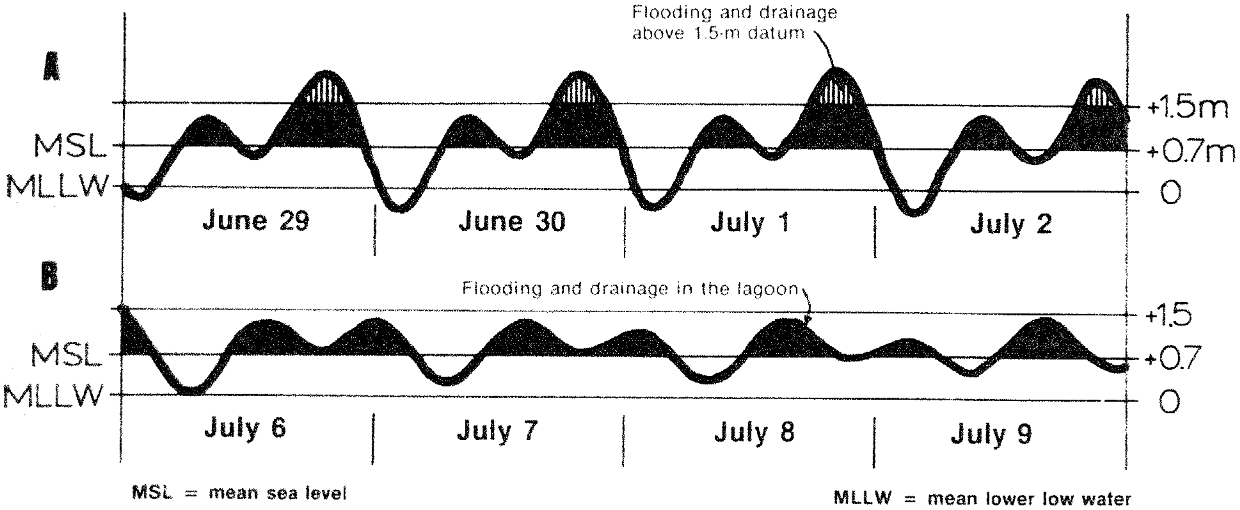


Figure 8. Tidal curves for several days in June and July 1981. (A) Curves for spring tides, showing times of flooding and drainage in the lagoon and times of flooding and drainage above the 1.5-m datum, the approximate lower boundary of the salt marsh. (B) Times of flooding and drainage during neap tides (from National Ocean Survey tidal curves for Outer Los Angeles Harbor).

tidal cycles and shortening the flood portion, which in turn is responsible for higher velocity currents on flood than ebb tides (i.e., the same volume of water must enter in less time). These currents are turbulent and provide good mixing. In the open expanses of water away from the mouth, tidal currents are slow and are probably insufficient to cause much mixing. However, these areas are shallow. Movements of water generated by even light breezes apparently are sufficient to cause mixing. In hundreds of dissolved oxygen determinations of water collected near the bottom in conjunction with primary productivity studies, anaerobic conditions (signifying no mixing) were never encountered (Shaffer 1982).

2.4 THE PHYSICOCHEMICAL ENVIRONMENT

Water Temperature

The physicochemical environment is strongly under the influence of the hydrological regime. The moderate temperatures of the ocean at the mouth govern the temperatures within the lagoon. Surface water temperatures measured at Zuma Beach, approximately 25 km to the southeast, range from 13°C to 18°C (monthly means), 12°C to 21°C (mean monthly maxima and minima), and 9°C to 22°C (absolute maximum and minimum) (California Water Resources Control Board 1979). Because of the rapid tidal flushing of the lagoon, factors operating within the lagoon are of secondary importance. However, in the shallower and more landward subtidal areas, air temperature and insolation become increasingly important. Of course, at the surface in the intertidal zone these factors have to predominate when the tide is out. For the emergent vascular plants of the salt marsh, this will be the great majority of the time.

No systematic measurements of water temperature within the lagoon have been made to evaluate the extent that air temperature, insolation, and depth influence temperature; however, two data sets suggest that the modifying effect of shallow depths can be substantial. Wilson (1980) made hourly measurements in the middle of the sand channel leading from the mouth of the lagoon into the eastern arm and 45 m away in the middle of a subtidal flat. At low tide the former was covered by 50 cm of water and the latter by 15 cm. For the 6 measurement days (all during summer), midwater temperatures at the deeper station always exceeded those at the shallower station at night (12 a.m. - 5 a.m.); during the day (10 a.m. - 3 p.m.) the shallow station was considerably warmer than the deeper station. Such temperature differences are striking and surprising, given the rapidly flowing waters of the sand channel.

DuBois (1981) related temperatures measured in the inner, broad, open water part of the eastern arm of the lagoon (termed subtidal pond by Warme [1971]) with ocean temperatures near the mouth of the lagoon. Even in the early summer morning when lagoon waters would have cooled to their greatest extent, temperatures were higher in the lagoon. In the winter, when day length is short and insolation is reduced, water temperature in the lagoon at night would be expected to be lower than offshore.

Salinity

No systematic measurements of salinity have been made in Mugu Lagoon. Given the virtual absence of surface flows of freshwater except during storms, there is every reason to expect dilution by freshwater to be brief. The abundance of long-lived stenohaline marine organisms suggests that even brief dilutions substantially below 34% are rare (Warme 1971); however, dilution by freshwater was almost certainly involved in the die-offs of the sand dollar Dendraster excentricus and the bubble shell Bulla gouldiana in 1969, 1978, and 1980. Unfortunately, salinity has not been measured at the heights of the storms when the reductions were greatest. The only relevant measurements were 19 and 28 ppt, 1 and 2 days respectively, after a 2-cm rainfall, culminating a 16-day rainy spell in which a total of 15 cm of precipitation had fallen (pers. observ.). Apparently, there is a rapid return to marine conditions.

Although Mugu Lagoon has close to marine salinities (34 ppt) most of the time, the three major divisions of the lagoon must differ somewhat. The eastern arm is the most nearly marine. It is virtually without a watershed, being flanked by a narrow sandspit on one side and a steep mountain on the other (a 440-m peak within 1.5 km of the edge of the lagoon). Furthermore, the opening to the ocean is closer than any long-lasting freshwater source (Figure 2). The central basin receives the major inlet stream, but this stream is channelized all the way to its point of discharge into an artificially deepened area, with a direct path from there out the mouth of the lagoon. Only in the western extremity of the western arm is a longer-lasting gradational salinity regime likely. This part of the lagoon is partly under the influence of the coastal plain. Because of the low relief, water runs off slowly even through the network of agricultural drainage ditches in the area (Figure 2). Also, the western part of the lagoon consists mainly of emergent marsh and long shallow channels, for the most part not confined by artificial levees. Here, freshwater inputs might be more persistent.

Dissolved Oxygen

Dissolved oxygen generally is high in the waters of the lagoon because of high tidal exchange rates and shallow depths easily mixed by winds. The only glaring exception is that reducing conditions often develop beneath senescent mats of the green algae Enteromorpha and Ulva, both in the deepest parts of the lagoon and in a wrack line at the edge of the marsh in late summer. This affects the underlying sediments but apparently does little to the overlying water.

Bottom Sediments

Warme (1971) and Biddle (1976) described the sediment characteristics of the eastern arm of Mugu Lagoon. There is no systematic appraisal of the rest of the lagoon. Within the eastern arm two sediment gradients exist. Generally, sediments become finer grained from west to east (increasing distances from the mouth) and south to north (from the sandspit, across the subtidal "ponds," and across the salt marsh). The west-east gradient is a function of the reduced velocities of tidally generated water currents at greater distances from the mouth. The south-north gradient is the result of a composite of factors.

The south shore of the lagoon is enriched in sand over what it would otherwise be by occasional overwash of material from the ocean beach. This happens when exceptionally high surf coincides with spring tides. Initially, the input of new sand is restricted to a small delta projecting into the lagoon. Subsequently, that sand is distributed by the longshore tidal currents along the whole south side. Even in the deepest parts of the subtidal ponds, sand (particles >63 µm in diameter) predominate over mud (Warme 1971). This suggests that water movements are strong enough even here to keep fine particles in suspension or remobilize them. The other possible explanation is that the source of fine particles is small compared to the source of sand. Aeolian deposition of sand by wind may explain further the prevalence of sand in the middle of the subtidal ponds.

Silts and clays predominate only in the salt marsh or in bare areas and depressions within the salt marsh (Warme 1971). Here, tidal currents are weak, because relatively small volumes of water are passing over any given point in a tidal cycle. Furthermore, the vegetation baffles currents and reduces the turbulence associated with waves that otherwise might cause the suspension and removal of fine particles. (This analysis is founded on the low input of fine sediments. In the aftermath of major storm-caused deposition of fine sediments in 1978, it is no longer applicable, as will be described later.)

Solar Radiation

In addition to its considerable influence on the temperature regime of a shallow aquatic ecosystem, solar radiation is even more important as a major determinant of primary productivity. Average daily incident solar radiation in the photosynthetically active region

(PAR, approximately half of the total incident energy in the visible spectrum) ranged from 18 Einsteins (E) per m^2 per day (E m^{-2} d^{-1}) in December to 56 E m^{-2} d^{-1} in May (Shaffer and Onuf 1985; Figure 9). The difference in day length from 10 to 14 h accounts for 20% of the increase, and the higher intensity of solar radiation caused by the higher angle of incidence during the summer accounts for most of the rest. Cloud cover and its attendant effects on solar radiation showed remarkably little variation over the year, even though all precipitation is in the winter (Figure 9). This small variation is because fogs are common in the summer. For organisms in the water column and on the bottom, turbidity attenuates the light further, in proportion to the concentration of suspended matter and depth. The effect is greatest over unconsolidated muddy bottoms and least over sand (Shaffer and Onuf 1983).

Nutrients

No data are available on nutrient concentration in the water column or in sediments. Inferences about the nutrient regime are deferred to Section 5.6, after other information about the ecosystem has been presented.

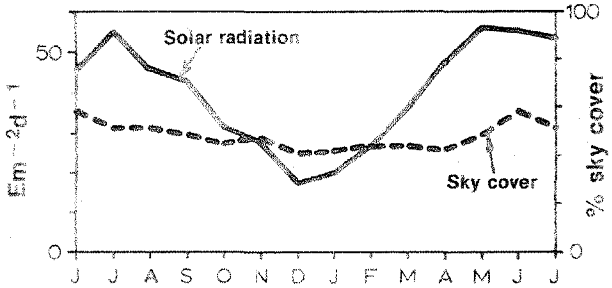


Figure 9. Mean daily solar radiation in Einsteins (from Shaffer and Onuf 1985) and sky cover (10-year average, January 1960 through December 1969; from de Violini 1975) in different months.

CHAPTER 3. PHYSIOGRAPHY

At Mugu Lagoon, the steep gradients in physical factors where land, sea and freshwater meet create a wide spectrum of different living environments in a small geographic area. The gradients that interact to create a mosaic of different habitat types were described in the preceding chapter: current velocities, substrate texture, light, elevation, time of submergence, salinity (occasionally), and temperature. Because of large changes in some of the factors after a major storm in 1978, the physiography of Mugu Lagoon is described in this chapter in two parts: before 1978 and after.

3.1 STRUCTURAL COMPONENTS— BEFORE 1978

The major structural features of the Mugu Lagoon ecosystem are the: (1) tidal inlet and delta, (2) subtidal channels, (3) subtidal ponds (Warme 1971) or permanent open water, (4) tidal flats, (5) tidal marsh, (6) tidal creeks, (7) salt pans, (8) natural adjacent upland (barrier spit), (9) adjacent upland that is disturbed open space, (10) developed adjacent upland, and (11) the nearshore Pacific Ocean. Features 1-7 are exclusively part of the estuarine ecosystem, whereas Features 8-11 are only marginally part of the estuarine ecosystem. Adjacent uplands are divided into three categories (Features 8-10), because they have distinctly different relationships with the aquatic part of the system. These relationships will be discussed only in the most general terms. Feature 11 is immensely more important than adjacent uplands as an influence on the lagoon, as is the influence of remote parts of the watershed transmitted by Calleguas Creek.

Tidal Inlet and Delta

This physiographic component is characterized by shallow depths (predominantly intertidal), the highest current velocities experienced inside the lagoon, and consequently, an unstable bottom of sand and shell fragments. Although small in area at any one time, the inlet and delta exert an influence over a much larger area in three ways. First, the inlet migrates along the spit. Second, the elevation of the inlet sediment bottom changes, and with it the depth, duration, and periodicity of inundation of areas inside the lagoon. Third, the inlet is a major source of sand for the lagoon.

All of these effects arise from the same set of processes, for the most part operating outside the lagoon. The movement of sand along the coast is mostly from northwest to southeast. Littoral drift of sand along a beach occurs when waves approach at an angle rather than perpendicular to the coast. Westerly winds strongly prevail in this region most of the time, as do the waves that they generate. Furthermore, the southward curve of the coast farther east (Figure 1) and the islands offshore block or moderate the impact of waves arriving from other directions. In consequence, sand originally supplied by the Ventura and Santa Clara Rivers is delivered almost continuously (but in varying amounts depending on wave conditions) to the northwest bank of the tidal inlet. This bank builds out into the channel, and accordingly, the southeast bank must erode if the same channel size is to be maintained. Hence, the inlet migrates to the southeast.

Of course, the same size inlet channel is not always maintained. For instance, when periods of high sand supply by littoral drift coincide with neap tides, the tidal inlet can fill partly or completely. Under those conditions, the small volumes of water moving through the mouth provide insufficient force to clear the added sand. Subsequent higher tides fill the lagoon, but less water will drain out than previously. Greater volumes will be retained at low tide; less mixing and exchange will occur. This condition will persist until extreme high spring tides move enough water fast enough to re-excavate the inlet channel.

Littoral drift and inlet migration assure that there is a considerable movement of sand and water into and out of the tidal inlet. However, because the speeds of tidal currents are higher during flood than ebb phases of the same cycle (see Chapter 2), more sand enters the lagoon than departs. This provides a supply of new sand to the lagoon and accounts for the flood-tide delta and the instability of the sand bottom.

Inlet migration at Mugu Lagoon is part of a repeating cycle of opening, migration, and closure. The following description draws heavily on John Warme's detailed analysis (1971). As the tidal inlet migrates toward the southeast end of the lagoon, the flood-tide supply of water for the entire lagoon must pass through a long and meandering channel. This retards delivery so that relatively little water can enter the lagoon before the high tide has passed. The resulting flows are insufficient to keep the mouth open, even on spring tides. Consequently, the mouth closes and remains closed until winter storms supply enough freshwater to overflow the barrier spit at its lowest point. Normally, the overflow will be near the head of the Mugu Submarine Canyon because its deep water causes the refraction of waves. This reduces their energy when they break on shore nearby, so that the berm of the beach is not built as high there. The breach erodes the spit and develops into a new tidal inlet. Inlet migration proceeds southeastward until the cycle is completed by another closure.

Apparently there were several cycles during the 1960's, when the Navy intervened to shorten the periods of closure by bulldozing a new channel shortly after the inlet closed (Warme 1971). Recently, the cycles have been somewhat different: a new tidal inlet formed opposite the mouth of Calleguas Creek before or just as the old inlet closed, some hundreds of meters southeast along the barrier spit. The northwest limit for the location of the inlet is fixed by the placement of riprap along part of the spit. The presence of well-established dune vegetation beginning approximately 1 km to the southeast indicates that this had been the down-current limit of inlet migration for a long time. Inspection of seven aerial photographs from 1959 to 1979 suggests that this was also the most common location of the inlet.

The most recently completed cycle of inlet migration did not follow the abovementioned pattern. This time the inlet migrated its usual 800 - 1,000 m between February and September 1980, remained there through June 1981, and then, instead of reinitiating the cycle opposite the mouth of Calleguas Creek, continued its movement to the southeast. By August 1981, the tidal inlet had moved another 150 m, and finally, in February 1982 the inlet closed after moving another 150 m. The inlet then reopened 1,300 m to the northwest. Before migration ceased, a 300-m strip of deeply rooted dune vegetation was destroyed. Presumably, this extreme cycle of inlet migration resulted from a major change in 1980 or 1981 in the coastal processes that move materials on, off, and along the shore.

Subtidal Channel

The only channel in the eastern arm of Mugu Lagoon that always has substantial flow links the tidal inlet and tidal delta with the subtidal ponds of the arm (Figure 10). The subtidal channel is quite uniform in width (approximately 50 m) but varies in length from 700 to 1,400 m according to the location of the tidal inlet and delta. The subtidal channel is 10-30 cm deep at low water for the most part, but occasional depressions approach 1 m deep. The bottom is more than 95% sand throughout (particles greater than 0.063 mm diameter). Maximal current speeds have not been measured

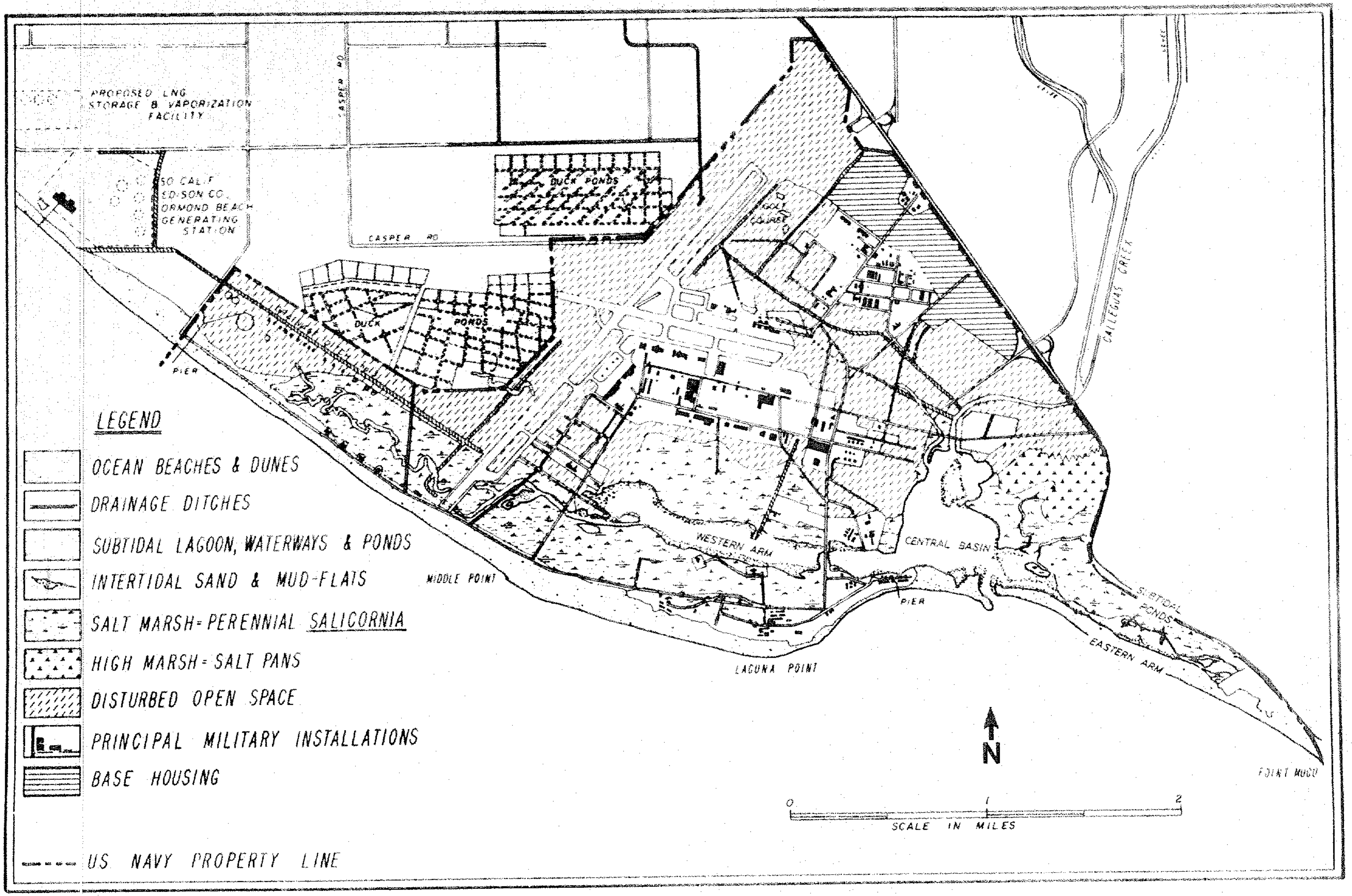


Figure 10. The main physiographic and land-use features of Mugu Lagoon (adapted from Macdonald 1976b).

in the subtidal channel; they are certainly less than those that can affect the tidal delta but much greater than speeds that affect other parts of the lagoon (except the adjacent intertidal sand flats). Currents are never powerful enough in any tidal cycle to shift more than the top few layers of sand grains in the subtidal channel, whereas much more extensive alterations are possible in a short time in the delta. The greater stability of the substrate in the subtidal channel is very important to the biota, as will become apparent in the next chapter.

Subtidal Ponds and Other Areas of Permanent Open Water

Areas of permanent open water make up about one-fifth of the Mugu Lagoon estuarine ecosystem; however, only the subtidal ponds of the eastern arm have been described in detail (Warme 1971; Figure 10). The greatest depth recorded along Warme's topographic transects was approximately -0.3 ft MLLW, which would correspond to a water depth of approximately 1.2 m at low water in the lagoon. Tidal currents are barely perceptible, except where the subtidal channel empties into the western pond and in the constricted areas between marsh islands and the adjacent mainland marsh. Often surface currents generated by the wind are more apparent than the tidal currents. Because of the slow movements of the water, much finer particles can and do settle out than in the inlet, delta, and channel environments.

The hydrodynamic environment allows for the accumulation of fine particles in the sediments in the subtidal ponds; nonetheless, sand continues to dominate even here. Sand content ranged from 50% to 90% by weight in Warme's (1971) samples from the subtidal ponds. In addition, the finer particles were confined to the surface layer (Figure 11). Finally, there was a dearth of intermediate sizes (evident in the abrupt change in slope of the cumulative percentage plots of grain-size distribution; Figure 11).

These characteristics suggest several things. First, two different sources of sediments and modes of their introduction into the ponds are implicated. Otherwise, fractions of intermediate size would be more evident. The sand fraction has its origin in the barrier spit and may be delivered by the wind. Certainly it is not carried suspended in the water. The predominantly clay fraction is terrigenous in origin, delivered to the central basin by Calleguas Creek and by tidal currents into the subtidal ponds of the eastern arm. Although coarser material undoubtedly is delivered to the central basin, the tidal currents are sufficient to transport only the fine fraction into the ponds of the eastern arm.

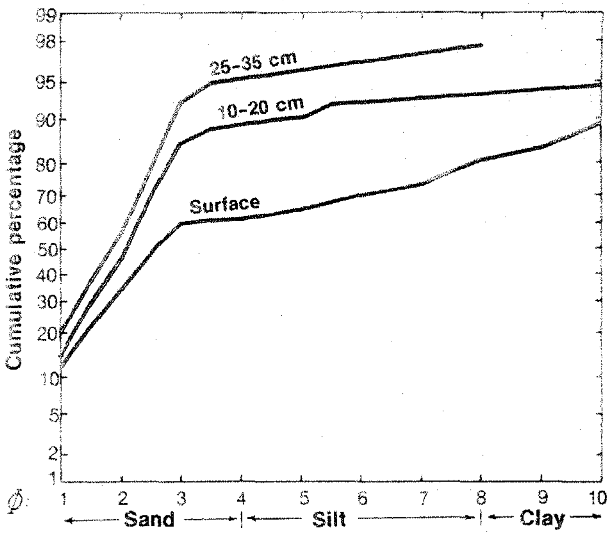


Figure 11. Variation in substrate texture with depth from a core taken in the middle of the eastern pond of the eastern arm, Mugu Lagoon (modified from Warme 1971).

The second conclusion to be drawn from these observations is that the supply of fine particles is small, at least relative to the supply of sand. Otherwise, fine particles should predominate, at least in the surface layers. (The predominance of sand at greater depths might only reflect a different depositional environment in prior times, such as ancient beach or dunes in existence before the formation of the lagoon.) The only other possibility is that the depositional environment is not what it seems; i.e., the "normal" situation of slow, weak water movements is violated often enough (by great water turbulence generated by high winds?) or is sufficiently modified (by activities of organisms?) to yield a sediment in some ways more characteristic of a higher energy environment. This latter alternative will be considered later.

Expanses of permanent open water in the central basin and the western arm of Mugu Lagoon differ from the subtidal ponds of the eastern arm in shape and other characteristics. The dredging of the central basin, the central basin's role as receptacle for the discharges of the only major inlet stream, and the separation of most of the central basin from the barrier spit (the source of sand) all should make for different environments than those just described for the eastern arm. The western arm has an almost uniform width from end to end except where a causeway constricts water to a narrow culvert system, and no direct communication with the barrier spit. This suggests that the western arm will be much muddier than the eastern arm because the culverts restrict tidal exchange and because no supply of sand is available from the barrier spit.

Tidal Flats

In the eastern arm, the tidal flats adjacent to the subtidal channel are subject to fast currents and are sandy, while those adjacent the subtidal ponds are subject to slow currents and have larger fine fractions. In both cases, the sediments are coarser on the barrier spit side than on the mainland side. In these ways the different kinds of tidal flats have much more in common with adjacent subtidal areas than with each other. In the western arm, tidal flats are predominantly silts and clays.

The bottom of the inlet to Mugu Lagoon is at approximately mean sea level. Immediately outside the inlet the time of tidal exposure increases continuously with increasing elevation, starting at zero at lowest low water (approximately -0.6 m MLLW). The distinction between subtidal and intertidal is blurred by the surf. In contrast, everywhere inside the lagoon the time of subaerial exposure jumps directly from zero to several hours at the subtidal-intertidal boundary, because the water level inside the lagoon remains at mean sea level the whole time that the tide is below mean sea level in the adjacent ocean. The boundary is not blurred much by waves washing up the shore. Above this boundary the time of subaerial exposure increases continuously with increasing elevation. Thus, there is no rarely exposed low intertidal zone in the lagoon. Being anywhere in the intertidal will mean at least several hours of exposure for each tidal cycle. Although the differences between exposed and submerged conditions virtually disappear only a few millimeters into the substrate, they constitute rigorous physiological challenges to the biota confined to the surface.

Tidal Marsh

The dominant feature of the tidal marsh is its vascular plants. The plants are terrestrial in origin; hence, it is not surprising that the marsh is confined to the upper part of the intertidal, where time exposed to the air exceeds time covered by water. Macdonald (1977) defined the lower limit of the tidal marsh as the elevation where time of maximum continuous submergence rises sharply from a level of about 7 h (Figure 12). Currents are slow in the marsh and are less at high elevations than low. Also, the vegetation retards flow and virtually eliminates wave action at the sediment surface. Consequently, some of the finest sediments in the lagoon are found here. Nothing is known about the conditions in the marsh surrounding the western arm; however, the gradient toward finer sediments at higher elevations may be reversed on the south side. Since the marsh is adjacent to the barrier beach, overwash and wind will supply large quantities of sand to the higher elevations here, except where development has eliminated the zone of contact (Figure 10).

Tidal Creeks

Tidal creeks deliver water to and from interior parts of the marsh. There are few at Mugu Lagoon, presumably because the marsh is narrow, being either confined by a mountainside as in the eastern arm or by artificial fill as in the

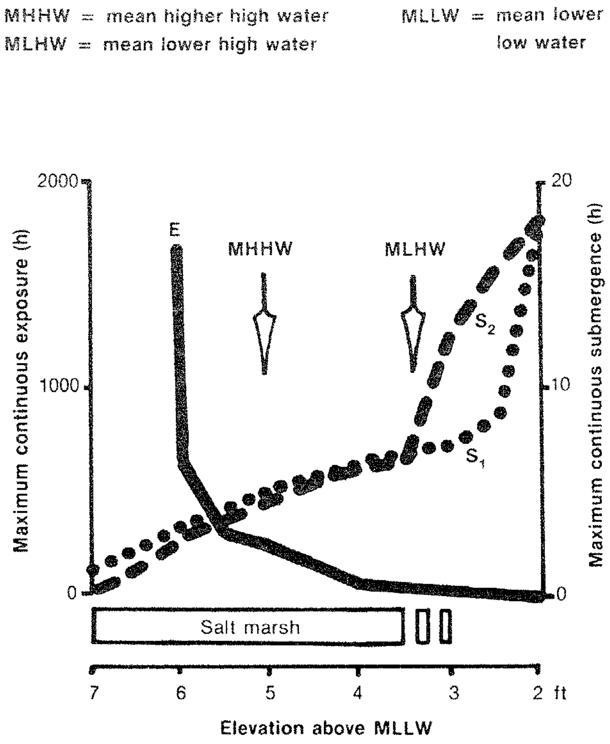


Figure 12. Duration of maximum tidal exposure (E) and submersion (S_1=Nov. 1964; S_2=Jan. 1965) for Mission Bay Marsh (adapted from Macdonald 1977).

western arm. Creeks are best developed in the marsh surrounding the western arm (see frontispiece). The bottoms of the tidal creeks can be as much as 1 m deeper than the adjacent marsh in their lower reaches and are subtidal (Warme 1971). Smaller creeks and the heads of the larger creeks differ less in elevation from the marsh and are intertidal. Currents in the creeks, especially currents in downstream portions, are faster than in the adjacent marsh. Consequently, the sediments should be coarser. Samples from a creek and from the marsh 75 m away were 33% and 6% sand, respectively (Warme 1966). Most of the tidal creeks are short (<0.5 km) because the salt marsh is narrow. The only long tidal channel extends approximately 4 km west from the western arm of the lagoon (Figure 10).

Salt Pans

These features are in the highest part of the intertidal zone in the one area of low slope that has not been altered by human activities (Figure 10, northeast from the central basin). Pans are located at an elevation approximately 2 m above MLLW and are very rarely inundated by tides. The highest are only reached by storm tides. Water stands in the pans for long periods. Therefore, there is considerable evaporation, leaving the salt behind and at the surface. Even if precipitation were more important than the tides in supplying water, the salts would still be left at the surface, thus accounting for the name "salt pan" and the absence of persistent vegetation.

Silt predominates in the salt pans and areas of high marsh immediately adjacent, unlike all other locations sampled in the eastern arm, suggesting the nearby Santa Monica Mountains as the localized source of the different sediments (Figure 13). In contrast, the tidal influence is so uncommon and, when it does occur, so slight, that tidal waters could not carry much suspended material (even clays) into the pans. Other samples relatively rich in silts, collected from the heads of tidal creeks near the Santa Monica Mountains (Warme 1971), are consistent with this interpretation.

Summary of Wetland Components

The tidal marsh has the greatest areal extent of all components of the Mugu Lagoon estuarine ecosystem, followed by permanent open water (accounting for less than one-third as much) and tidal flats (accounting for less than one-half that of open water; Table 2). The western arm is relatively rich in tidal flats, marsh, and creeks, whereas the central basin is decidedly poor. In contrast, the central basin has much more permanent open water, and the eastern arm has almost all the salt pans.

These differences in proportions are hardly surprising in view of the topographic features of the different parts of the lagoon coupled with their cultural history. Thus, notwithstanding major losses of tidal marsh to the development

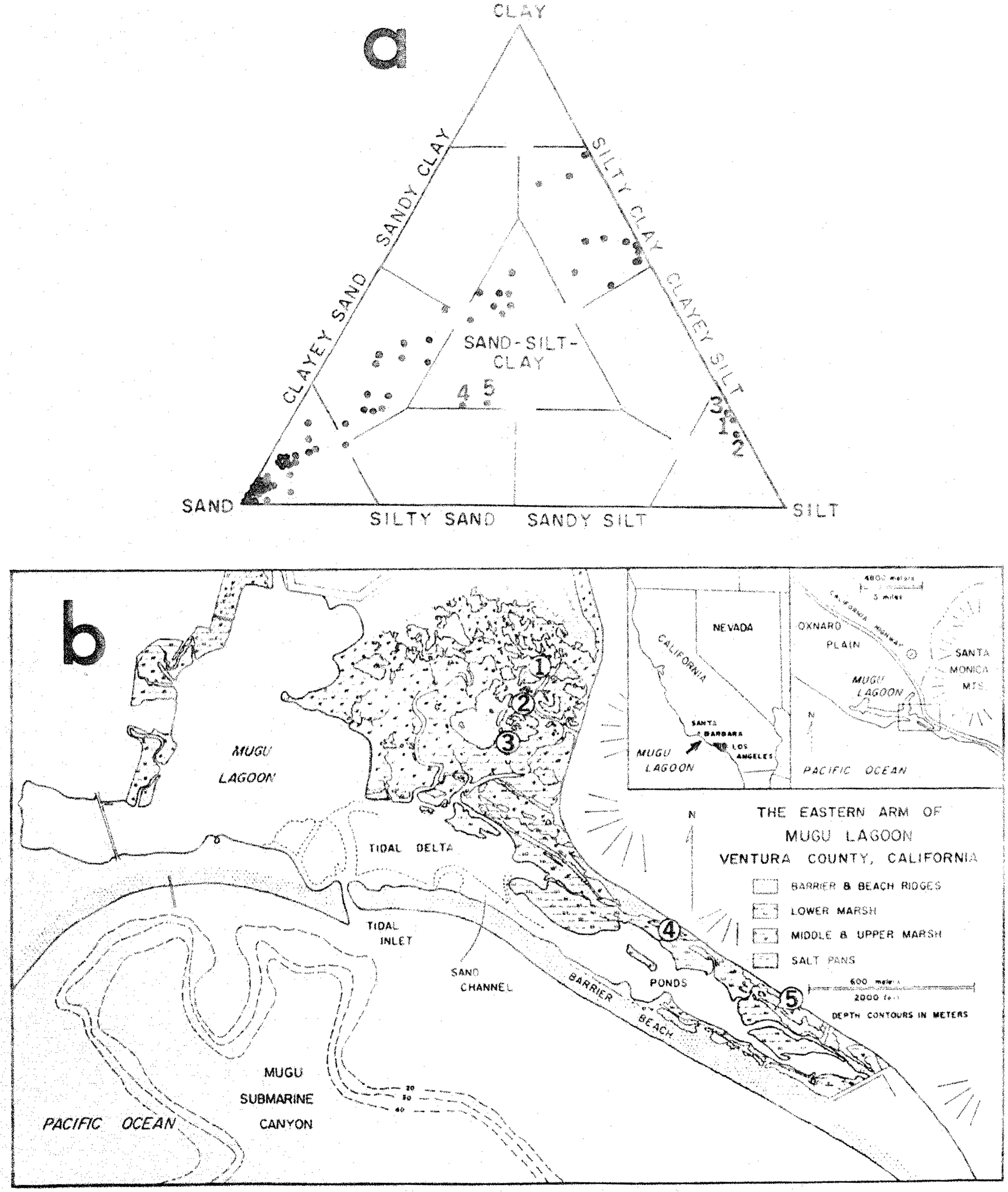


Figure 13. (a) Sediment triangle and (b) map showing samples in which silts were relatively enriched in surface sediment samples in the eastern arm of Mugu Lagoon (adapted from Warme 1966, 1971).

Table 2. The structural components of the Mugu Lagoon estuarine ecosystem: their area and distribution within the ecosystem (subtidal and intertidal components) and the length of edge of adjacent upland. (Based primarily on Figure 10.)

				% of the total for the whole lagoon lying within:		
Component	Area (ha)	Length (km)	% of total	Eastern arm	Central basin	Western arm
All subtidal and intertidal	597		100	22	16	62
Tidal inlet and delta	5		1		100	
Subtidal channel	5		1	100		
Subtidal ponds or permanent open water	111		19	14	54	32
Tidal flats	52		9	17	15	68
Tidal marsh	382		64	18	5	77
Tidal creeks	11		2	18		82
Salt pans	31		5	97	3	
Upland: all		22.2	100	24	11	65
Natural (barrier spit)		5.9	27	34	8	58
Disturbed open space		7.8	35	10	21	69
Developed		5.9	27	0	2	98
No interaction with wetlands		2.6	12	100[a]	0	0

[a] Most of the upland edge on the landward side of the eastern arm is excluded because it was always so steep as to have little role in the estuarine ecosystem.

of the Naval Air Station, the floodplain setting of the western arm still leads to a prevalence of intertidal components compared to the undeveloped eastern arm, which is pressed against a mountain flank. Presumably, salt pans were prevalent at the upper fringe of the marsh in the western arm, but were filled when the base was constructed. In the central basin, dredging eliminated the lower parts of the intertidal, while fill eliminated the upper parts. The consequence was the overwhelming predominance of permanent open water there.

Adjacent Uplands

The three categories of adjacent uplands have distinctly different relations with the aquatic components of the ecosystem. Adjacent upland in a nearly natural condition is limited to the barrier spit and beach. It is a major source of sand for the lagoon. The coastal strand and dune communities on the spit are important because of their rarity in the region; in addition, they provide habitat for a relatively small variety of organisms that also use the lagoon. Disturbed open space, modified by past human activity such as filling or diking, may be mowed or disked occasionally, but for the most part is left alone. As with the barrier spit, it provides alternative habitat for a small variety of organisms that use the lagoon. The organisms that use these two kinds of upland-wetland transitions probably are different. The developed upland, on the other hand, can be a source of inputs (pollutants, noise, and rapid movement of planes, vehicles, and people) that may reduce the utility of adjacent wetland for the biota normally associated with upland-wetland fringes.

The amount of edge between each kind of upland and its adjacent wetland would seem to be of greater significance than the area of upland in determining upland contribution to the estuarine ecosystem. Obviously, the width of the bordering upland also matters, but the use of adjacent upland by estuarine organisms probably is a rapidly decreasing function of distance from the edge. Until we know much more about what goes on landward of the upland-wetland edge, the length of the edge will have to serve as the best first approximation of the contribution of each kind of upland.

The three major lobes of the lagoon differ radically in amounts of the three kinds of edge. Virtually all of the developed edge is in the western arm, and the eastern arm is proportionately rich in natural edge. Despite the concentration of development in the western arm, natural and disturbed open space account for 60% of the upland-wetland edge. The role of roads is variable. The Pacific Coast Highway, skirting the northern side of the eastern arm (Figure 10), is fringed by a jumble of rocks and an almost-continuous wall of vegetation that differ little from the original border of rock rubble and vegetation at the foot of the Santa Monica Mountains. The heavily used causeway crossing the western arm should perhaps be regarded as the extreme example of a developed edge.

3.2 STRUCTURAL COMPONENTS—AFTER 1978

Sediment deposition caused a drastic transformation in the central basin of Mugu Lagoon sometime between 10 March 1977 and 16 May 1978. This transformation is illustrated in the series of aerial photographs appearing as Figure 14. On the former date the central basin was almost exclusively permanent open water. Tidal flats were limited to a small delta at the mouth of Calleguas Creek and the delta associated with the tidal inlet. Together they were less than one-third of the area of permanent

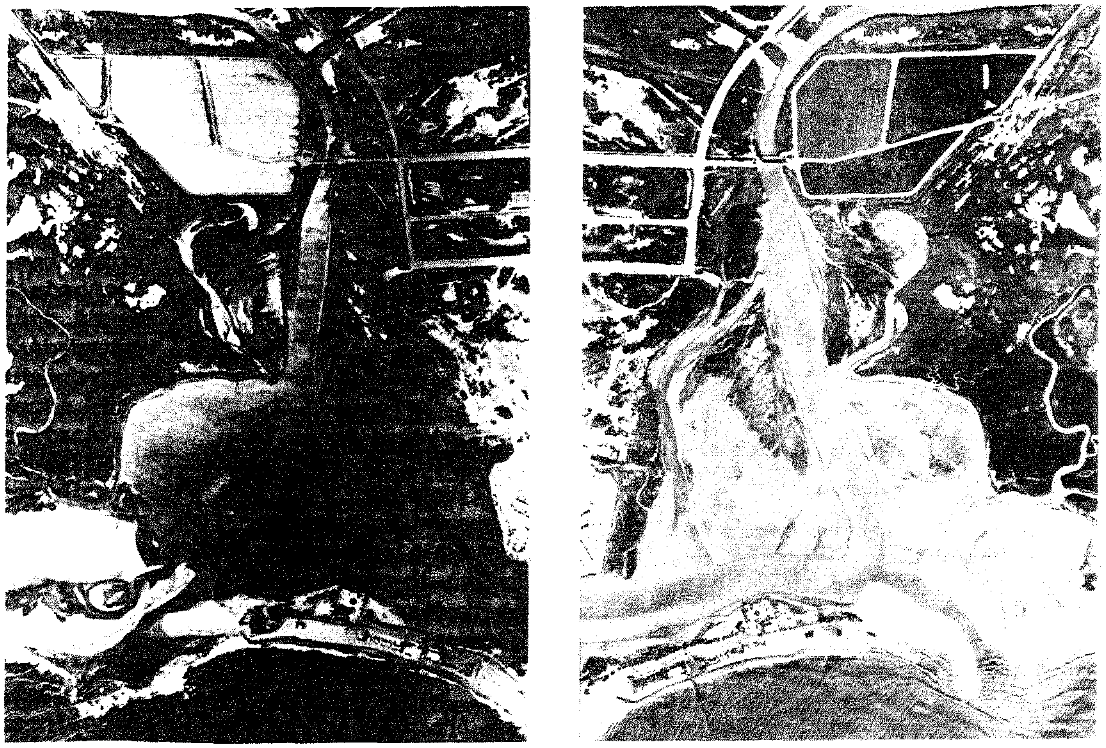
1971 **1977**

Figure 14. The extent of intertidal flats in the

open water. By 16 May 1978, the proportions were almost reversed. There was twice as much area of tidal flats as of open water. Between those two dates was the wettest season in the 36 years of the Point Mugu meteorological station, including one protracted series of storms that dumped 20.7 cm of precipitation in 9 days (5-13 February 1978). Effects of the storm series were not limited to the central basin. Sediment samples and depth measurements of the lagoon (the eastern arm in particular) from the 1960's (Warme 1966), from the 1978 storm period (Jill Cermak, University of California, Santa Barbara; unpubl. rep.), and from recent work (Onuf and Quammen 1983; Shaffer and Onuf 1983) have allowed us to reconstruct a fairly complete description of the effects of the storm.

The most obvious consequence of the storm was that the bottom immediately changed over most of the eastern arm from being predominantly sandy to being much finer grained (Figure 15). Although some of the fine material at the surface was selectively removed shortly thereafter, only the sandy-bottomed subtidal channel had reverted to its former condition by three months after the storm (Figures 15 and 16). Samples collected over a longer period on tidal flats bordering the subtidal channel (Sites 5 and 6, Figure 16) and on inner lagoon subtidal and intertidal areas (Sites 8 through 11, Figure 16) indicate that the much finer surface sediments deposited during the storm still persist in the inner lagoon pond area but no longer in the channel area (Figure 17).

In addition to the sediment changes that have lasted at least 2 years in the subtidal pond, the sedimentation also resulted in a substantial decrease in the depth of the lagoon. If it is assumed that all the change in elevation between Warme's (1971) original topographical transects in the mid-1960's and the resurveying of the same general areas in 1979 resulted from the February 1978 storm, then Figure 18a shows the extent and distribution of filling caused by



1978 **1983**

central basin of Mugu Lagoon in different years.

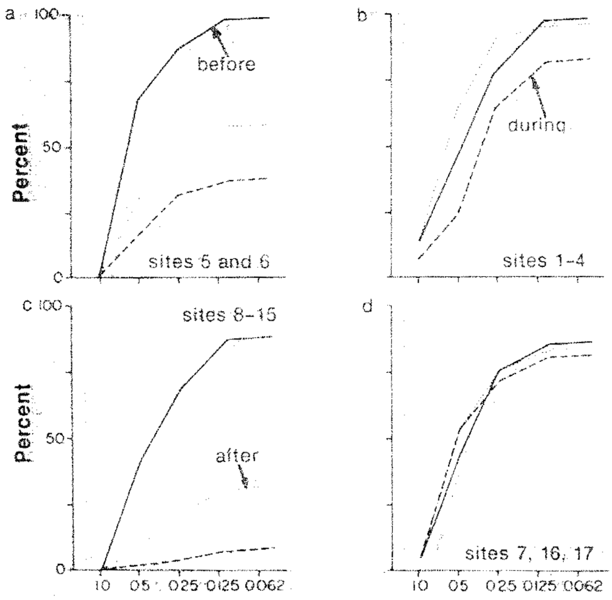


Figure 15. Sediment texture before, during, and after the major series of storms in 1978; sites grouped according to similar histories of change. (a) coarse to fine; (b) coarse to intermediate to coarse; (c) intermediate to fine; (d) little change. Sample sites are shown in Figure 16.

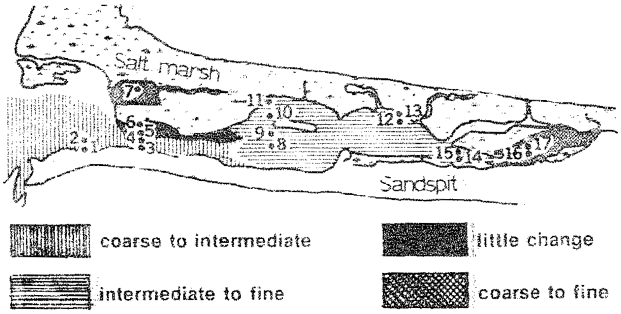


Figure 16. Sediment-sampling sites and areas of the lagoon with similar sediment changes in response to the major storm of February 1978. See Figure 15 for examples of the sediment-size distributions of the different areas over time.

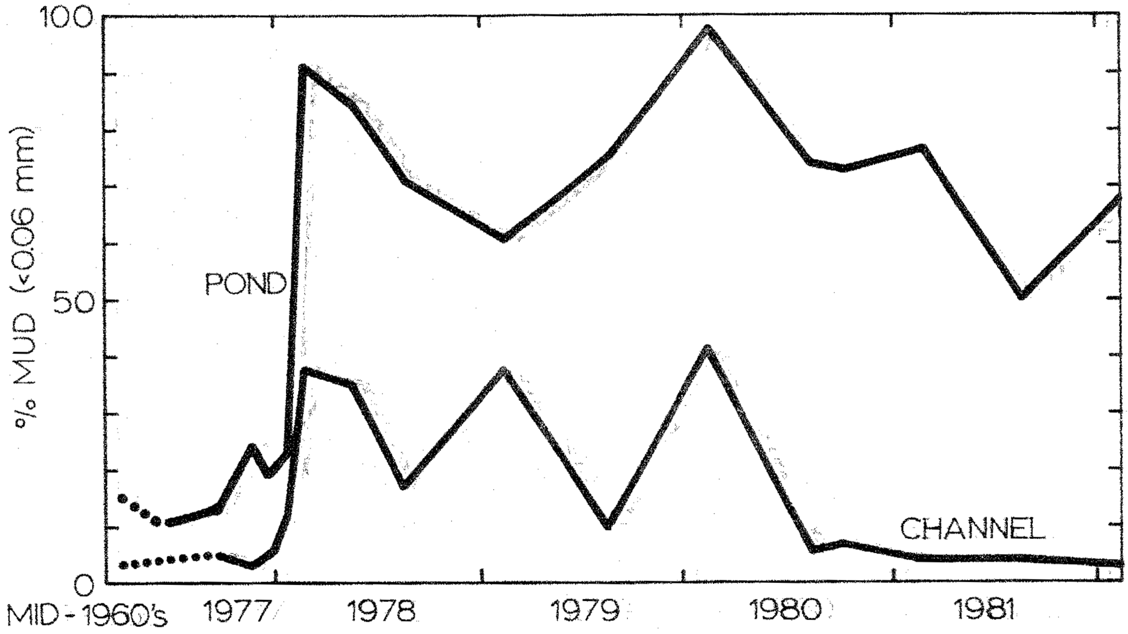


Figure 17. Changes in surface-sediment texture at sites in the tidal channel and western pond (near sites 5 and 6, and sites 9, 10, and 11 of Figure 16, respectively) of the eastern arm, Mugu Lagoon.

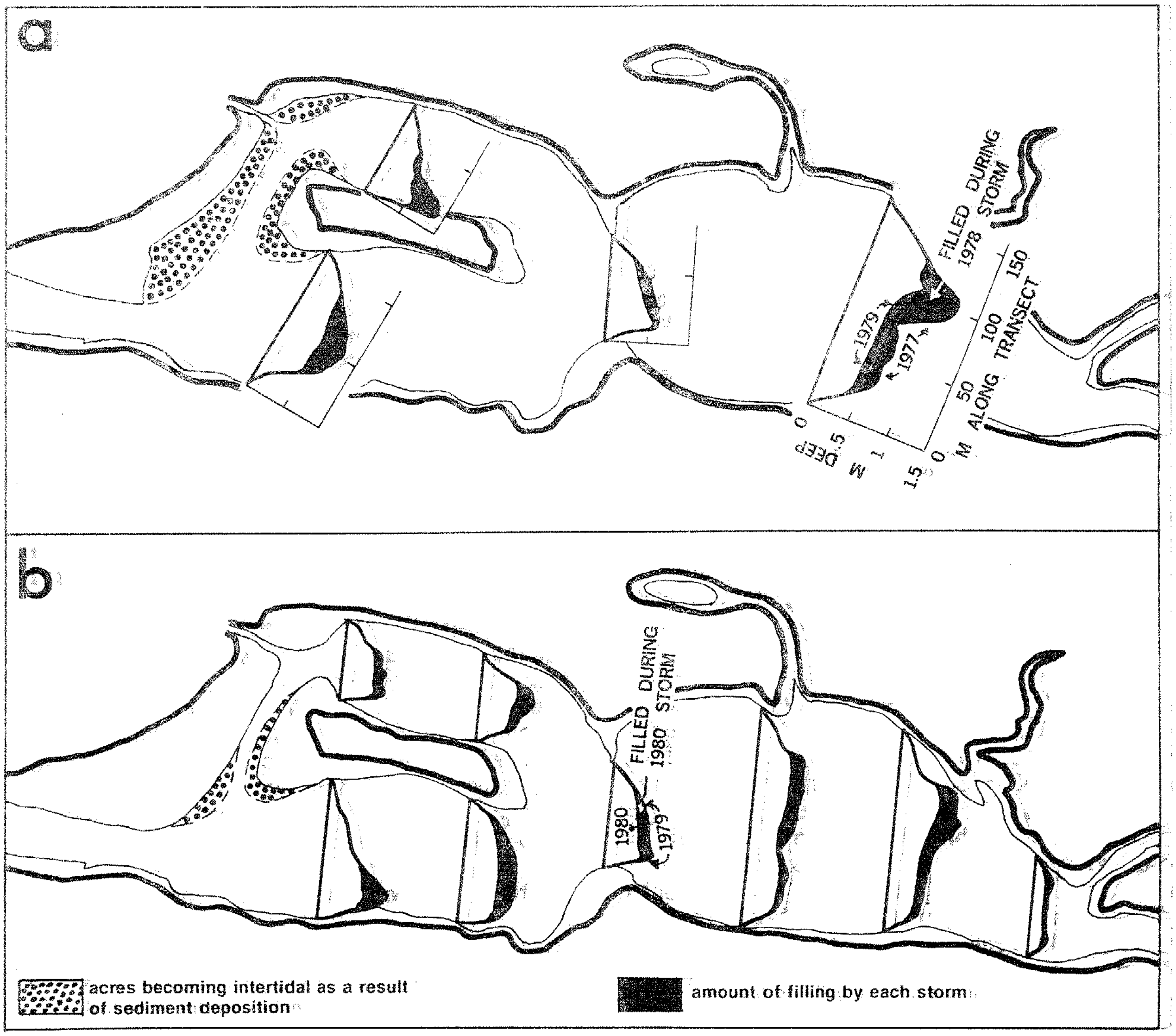


Figure 18. Changes in depth of the eastern arm of Mugu Lagoon, caused primarily by the storms of (a) February 1978 and (b) 1980.

that storm. According to this analysis, the average depth of the lagoon (at low water) has decreased approximately 13 cm (25%), and the deepest areas were filled the most.

Any comparisons between surveys made so many years apart contain uncertainties. Confidence in the interpretation that the one storm accounted for most of the change derives from the close agreement between the bathymetric changes inferred from surveys made many years apart and the few direct measurements of the new mud layer made in the same locations. In these cases, we know from samples collected as few as 17 days before the storm and collected again at the same sites as few as 3 and 13 days after the storm, that approximately 10 cm of loosely consolidated pure mud (over 90% by weight <0.063 mm in diameter) had been deposited on top of a compacted muddy sand (<25% by weight of particles <0.063 mm). (Compare February 1978 with January 1978 in Figure 17.)

The 4.5-yr record of Figure 17 includes more than one storm event. The peaks in both the pond and channel areas in February 1980 were the result of another major episode of storm-caused sediment deposition rather than the reworking of surface sediments. About half as much material was deposited overall as in 1978 (Figures 18a, b), and its effect was again short-lived in the channel (Figure 17). The return to coarse sediment was superficial, however. Thick bands or lenses of dense clay at varying depths within the sediment still show up in our infaunal sampling in this area. In the subtidal pond the change in sediment composition was minor, but the effect on depth was substantial and cumulative with that of the 1978 storm (Figure 18b). Together the storms have reduced the average depth and volume of the lagoon at low water by almost 40%. As in 1978, deeper areas were filled preferentially, thus reducing the topographic relief of the ponds still further.

3.3 MAJOR STORMS IN 1978 AND 1980 VS. 1962 AND 1969: DIFFERENCES IN THEIR EFFECTS ON THE EASTERN ARM

No aquatic system can sustain 40% reduction in depth in periods as short as three years (as did the eastern arm of Mugu Lagoon) and survive long as an aquatic system unless the events that cause such filling are very unusual. Consistent with this interpretation, there is no evidence of major depositions of fine sediments in the eastern arm prior to the 1978 storm. However, completely contrary to this interpretation, the storms of 1978 and 1980 were not the only major storms in recent years. There were larger storms in February 1962 and January 1969. Why did the later storms leave behind thick blankets of fine sediments while the earlier, somewhat more severe storms left no trace?

The possibility that deposition occurred, but that all traces were obliterated before trained observers were on hand to document the deposition, is untenable. MacGinitie and MacGinitie (1969) conducted their fieldwork in Mugu Lagoon from 1962 to 1964. They noted the 1962 storm and described some of its effects in other parts of the lagoon, but they explicitly stated that the eastern (southern in their terminology) arm was not affected. John Warme (1966), conducting his Ph.D. research in the eastern arm, would have described the site very differently if the February 1962 storm had caused substantial deposition of sediments. Although Peterson (1972) dealt only with the subtidal sandy habitat of the eastern arm, most of which would have been sandy again by his initial sampling in the summer of 1969, his study area included part of the subtidal pond near sites 8 and 9 of Figure 16. According to our experience, these sites would have remained muddy throughout his study if the January 1969 storm had caused sediment deposition. Apparently, these large storms, unlike the two major storms since then, did not cause much sediment deposition in the eastern arm.

As presented originally in Onuf and Quammen (1983), four factors alone or together might explain why the later, smaller storms caused massive sedimentation in the eastern arm of Mugu Lagoon, whereas the earlier, larger storms did not.

(1) The geomorphology of Mugu Lagoon is such that storms could not have major effects on the eastern arm if they coincided with neap tides. This is because the only path by which the sediment-laden storm waters of Calleguas Creek can enter the eastern arm is through the long, narrow subtidal channel (Figure 19). The more direct path is straight out the inlet. Furthermore, there is little flow into the eastern arm, because the rise in the tide is small. In contrast, when the marsh is flooded by a spring high tide, the lagoon has more the shape of a funnel aimed toward the east (Figure 19), and there is no obstruction to the passage of sediment-laden waters. In addition, the volume of water from which suspended matter can be sedimented is much larger than on a neap tide. According to our topographic surveys that included the marsh as well as the lagoon, approximately 3.7 times as much water moves in and out of the eastern arm on a spring tide as on a neap tide. Since the 1969 storm, as well as those of 1978 and 1980, coincided with spring tides, it would

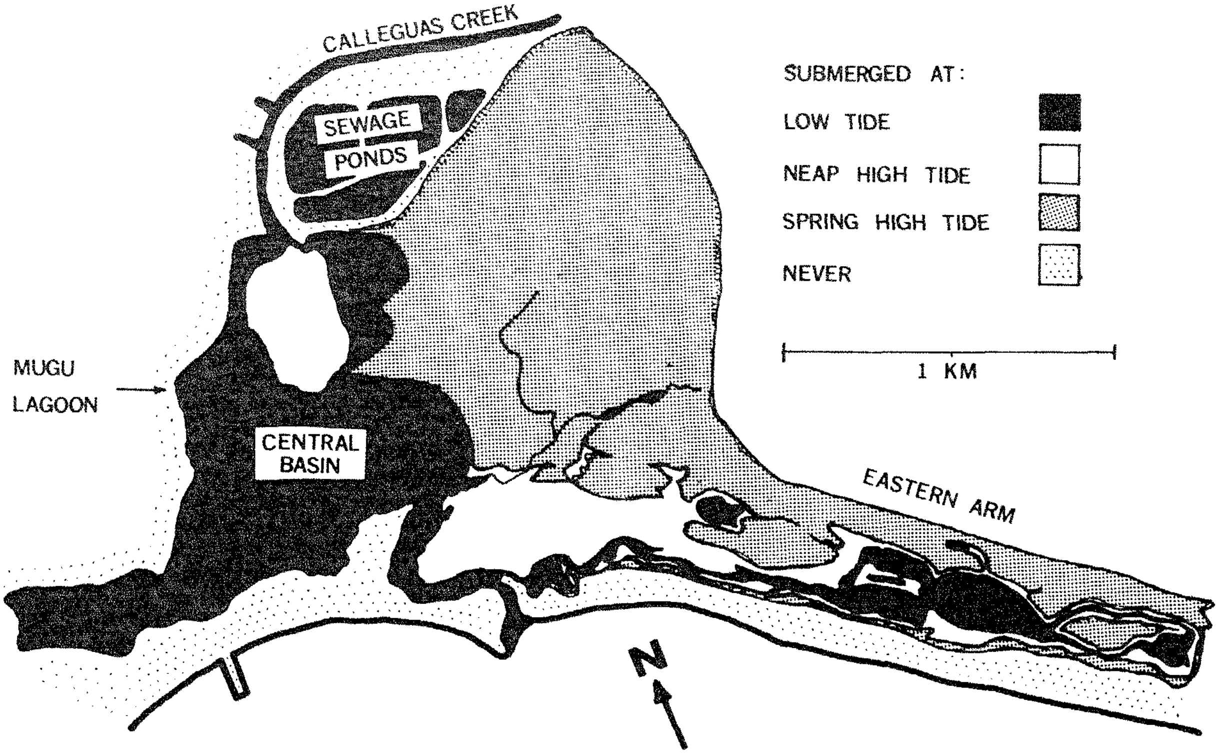


Figure 19. The relationship of the eastern arm of Mugu Lagoon to inputs from Calleguas Creek under different tidal conditions.

appear that this is a necessary but not sufficient condition for storm-caused sedimentation in the eastern arm.

(2) The earlier storms occurred during times when the erosion potential of the watershed was low. Erosion, and consequently the sediment load of streams, will be highest when the watershed is already near saturation before the major storm and when the vegetation of the watershed is in poor condition after a succession of dry seasons. Both the 1978 and 1980 storms were preceded by unusually wet months, while both the 1962 and 1969 storms were preceded by months of normal or subnormal precipitation. The condition of the vegetation in response to prolonged drought is harder to assess. Steffen (1982) proposed the cumulative deviation from the long-term average precipitation as a meaningful measure of vegetation condition. Here the critical feature is the length of time into a long-term period of drier or wetter than normal conditions (downward and upward trends, respectively, in the plots of cumulative deviation from the long-term average precipitation). The first 31 years of rainfall records for Point Mugu show a major drying trend (Figure 20) in which wetter than normal years are few and not in succession. Judging from the records of the nearby Oxnard weather station, the beginning of the Point Mugu record was the beginning of this dry period; thus, the major storms of February 1962 and January 1969 were one-half and three-quarters of the way through the dry period. While they were major storms, they certainly did not end the dry spell. That was left for a succession of wetter than normal years beginning 9 years later, of which the February 1978 and 1980 storms were a major and early part.

These results suggest that drought-caused deterioration of the vegetation in the watershed could have contributed to the greater sedimentation resulting from the later storms. This conclusion requires that vegetation is appreciably

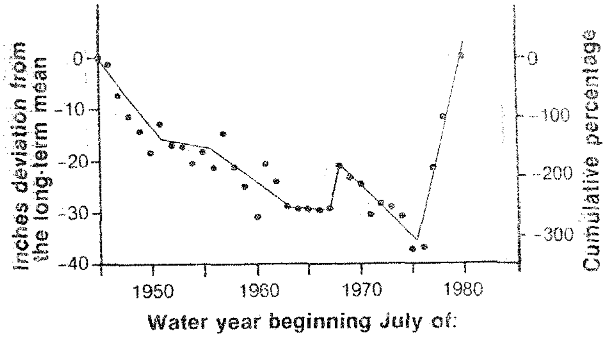


Figure 20. The cumulative deviations from the long-term mean precipitation (34-year record) at Point Mugu, California (based on de Violini 1975 and unpublished records). See Figure 6 for longer time series in the region. A downward trend of points indicates precipitation below the long-term average (1945-63, 1968-76); a horizontal series indicates precipitation equal to the long-term average (1963-1967); and an upward trend indicates precipitation above the long-term average (1976-1979).

less capable of retarding erosion after a dry period has been in progress for 32 years (as in 1978), compared to 23 years (as in 1969), and that more than 2 years of above-normal precipitation must ensue before the vegetation improves enough to retard erosion effectively. Otherwise, major sedimentation should not have occurred in 1980. Both requirements are plausible but lack independent verification.

(3) Development of the watershed since 1969 resulted in more erosion than during the 1960's. Baring soil on steep slopes will certainly accelerate erosion; this is happening in the watershed of Mugu Lagoon on a massive scale (Figure 21) for reasons stated in Chapter 1. This activity has become much more widespread since 1969 than before and could account for the difference in effects between the earlier and later storms.

Figure 21. Aerial photograph of hillside development near Moorpark, California, 1979.

Changes in land use before and after 1969 have been determined from maps and photographs for the part of the Calleguas Creek watershed lying within the Moorpark, California, U.S. Geological Survey topographic quadrangle (Figure 22). According to this analysis, of all hillside areas developed by 1979, 25% had been developed by 1947; another 15% was developed in the 22 years to 1969; and the remaining 60% was developed in only 10 years from 1969 to 1979. This corresponds closely to the largest area of "high rates of accelerated erosion" (caused by human activities) identified by Steffen (1982) and probably is representative of all areas so designated (Figure 23). He estimated that accelerated erosion might account for 40% of sediment generated in the Calleguas Creek watershed and even more in the remaining 18% of the whole Mugu Lagoon watershed; therefore, these changes in land use undoubtedly were responsible for large increases in the amount of sediments that were transported to Mugu Lagoon by major storms in 1978 and 1980, compared to 1969 and earlier.

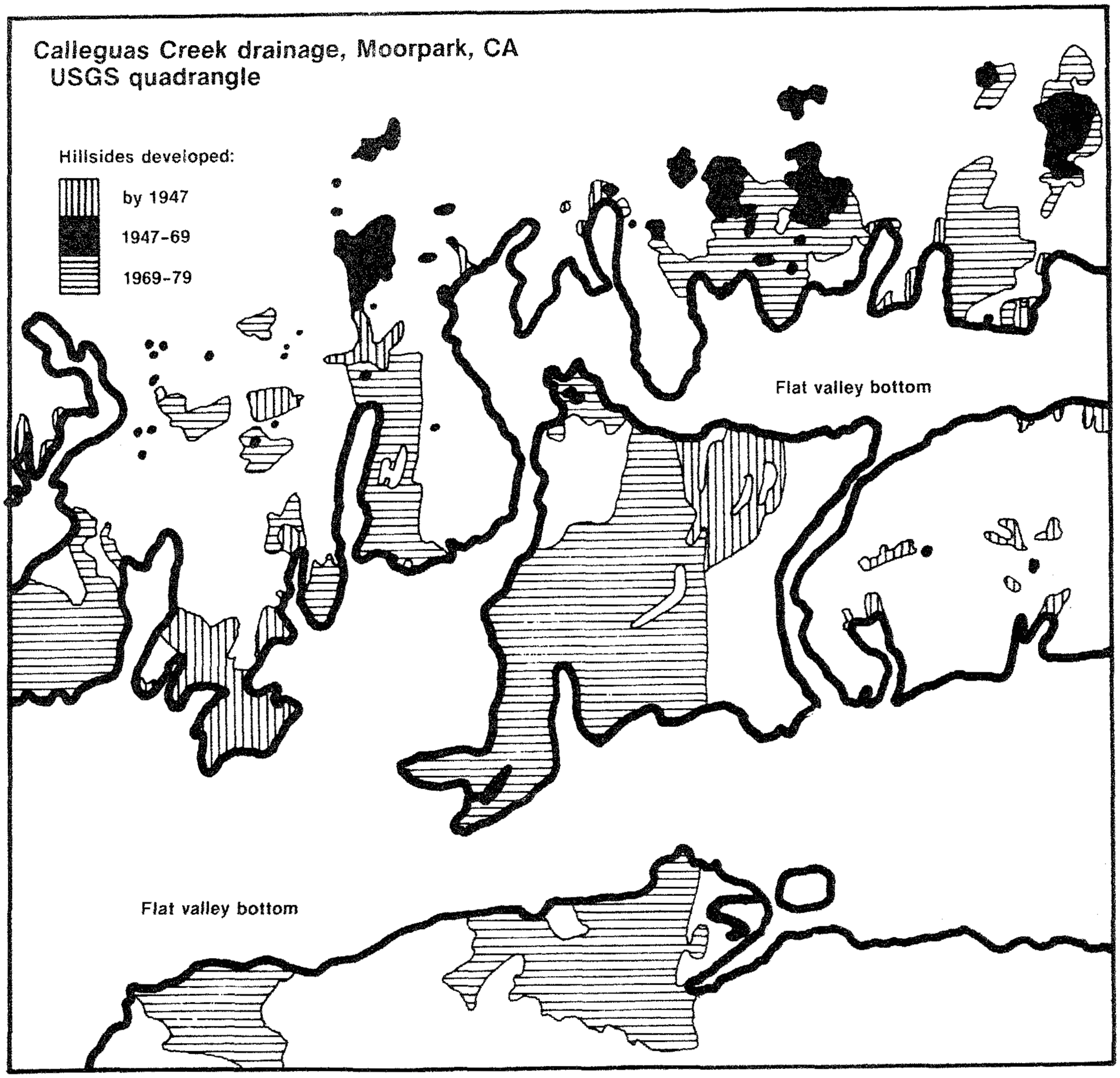


Figure 22. The extent of hillside development in one part of the watershed of Mugu Lagoon at different times (see dashed area in Figure 23).

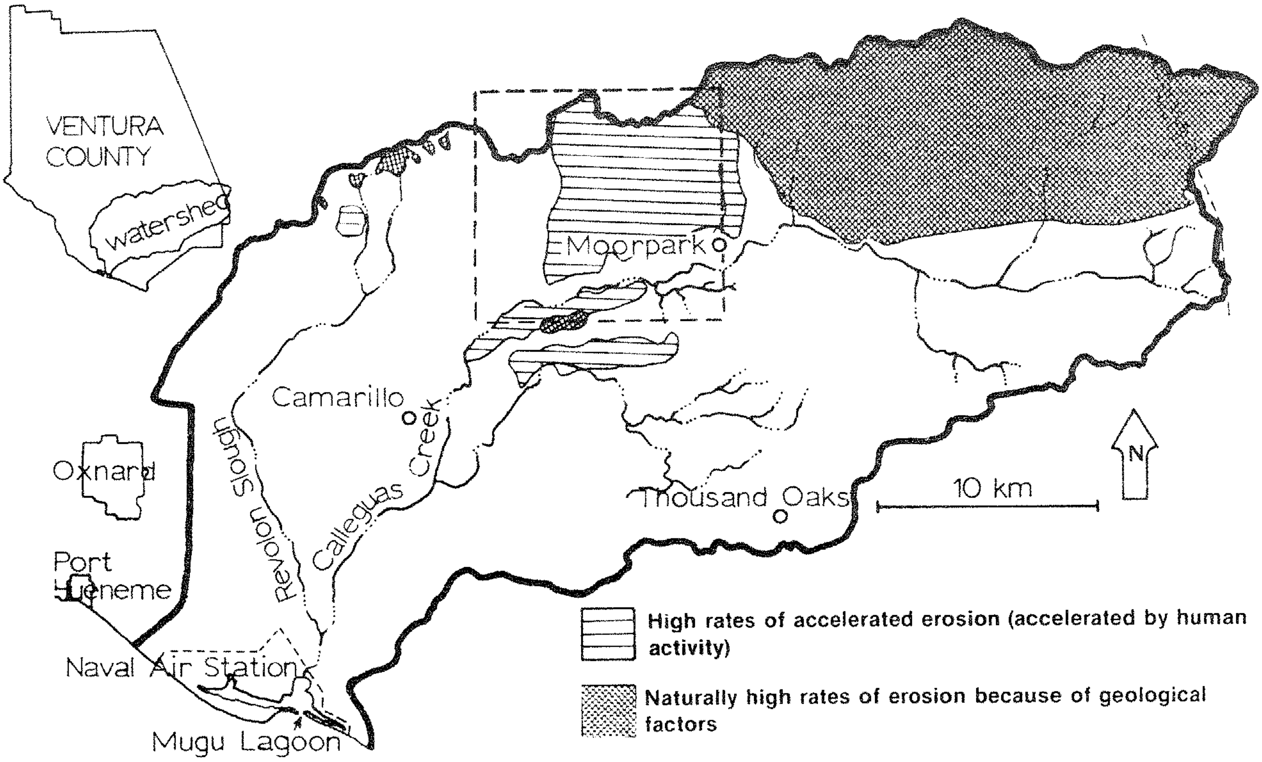


Figure 23. Areas with high rates of accelerated and geologic erosion (from Steffen 1982). Dashed lines indicate the area represented in Figure 22.

Accompanying the impacts of sedimentation has been a catastrophic reduction in certain groups of the lagoon benthos due to the reduction of salinities. With increased development and storm runoff, these catastrophic reductions may be caused by smaller storms than in the past.

(4) The central basin had a greater capacity to receive storm sediments during the 1960's. Until 1977 the central basin was a large expanse of open water (Figure 14) having been dredged approximately 10 m deep in the early 1960's. The storm flows leaving the narrow confines of the levees on Calleguas Creek would have spread out and slowed at this point, perhaps enough so that sediments could have settled within the central basin rather than within the eastern arm. A small delta was present at the mouth of Calleguas Creek at this time, and loose mud was observed in the central basin but not in the eastern arm after the 1962 storm (MacGinitie and MacGinitie 1969). The central basin ceased to be a body of open water during the 1978 storm (Figure 14), after which it ceased to be a sink for suspended particulates before they could reach the eastern arm.

This then can explain the different impacts of the 1962 and 1969 storms versus those in 1978 and 1980: until the central basin ceased to serve as a sediment trap, no storm could cause major deposition of fine sediments in the eastern arm. This explanation also resolves the dilemma of why a storm-dumped layer of mud could persist where the bottom created by "natural" processes (movements of water and air) had been predominantly sandy. The subtidal ponds always were a place where fine material could settle and stay. The reason that fine material constituted so little of the bottom was that the source of supply was small relative to the supply of sand from the barrier spit. With the filling of the central basin, the supply of fine material carried as far as the eastern arm by storm flows has increased and the amount of fine material deposited on the bottom of the eastern arm has increased as well.

The filling of the central basin is the proximate explanation for the abrupt and large change in the sediment dynamics of Mugu Lagoon in 1978. However, the other three factors cannot be ignored: (1) the phasing of storms with the tides will determine to what extent sediments are transported into the eastern and western arms from now on; (2) the condition of the watershed in response to the climatic cycle will determine how much soil is eroded; and (3) continued development of steep hillsides has been and will continue to be a major determinant of the sediment supply. The supply of sediments will probably increase as more hillsides are developed; this will be compensated in part by the vegetative cover during the wetter-than-normal period, but this condition will be temporary. Filling of the lagoon will continue, especially if storms coincide with spring high tides.

CHAPTER 4. THE BIOTA: DISTRIBUTION AND ABUNDANCE

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and
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The biota of Mugu Lagoon is rich in species. Forty-six vascular plant species, over 190 species of benthic invertebrates, 39 fish species, 198 bird species, 11 species of reptiles and amphibians, and 41 mammal species have been recorded in the lagoon and surrounding wetlands (this report; Macdonald 1976b; Natural Resources Management Office, U.S. Naval Air Station, Point Mugu, unpubl. list). This allows for a multitude of associations and interactions between species as well as with the physical environment. In this chapter we provide a description of the spatial and temporal distribution and abundances of the organisms, including the effects of the storm-altered physiography. We leave to Chapter 5 the discussion of what those organisms do (especially to each other) and how their functioning provides much of the organization that justifies the concepts of "biotic community" and "ecosystem."

4.1 THE PLANTS

The plants of Mugu Lagoon range from single cells drifting in the water to small shrubs rooted 1 m deep or more into the ground. Some are strictly limited spatially, while others appear to have no limits within the tidally influenced area. Some achieve such dense cover that they provide most of the physical structure of the environment for other organisms. Others, such as the microbial plants of the so-called "barren zone" of the tidal flats (Warme 1971), don't even appear to occupy a site; yet these plants may be almost as productive of new organic matter as the visual dominants and perhaps are much more productive of organic material available for assimilation by consumers (Peterson and Peterson 1979). Finally, all vary considerably in abundance or biomass seasonally and over longer periods. In some cases, the overwhelming dominant of one time may be hard to find the next and may be unimportant 1 year later.

Table 3 represents one attempt to depict this variety in a way that displays the obvious patterns. In the body of the table the symbols are an indication of the relative importance of each plant group in a habitat incorporating trophic (productivity, availability to consumers, nutritive value) and structural (influences on the physical environment, provision of habitat for other organisms) considerations. The criteria are most objective for comparisons of the same plant species in different habitats and correspond closely to biomass. Comparisons between different plant species, especially between different general categories of plants, are necessarily more subjective.

Phytoplankton, Benthic Micro- and Macroalgae, and Submerged Vascular Plants

Despite the large extent of continually submerged habitats within the lagoon, the contribution of phytoplankton in numbers and biomass is tiny. This is true even within the water column, the one place phytoplankton might be expected to dominate. This conclusion is based on three lines of evidence: (1) Benthic diatoms

Table 3. The relative importance (see text) of different categories of plants in the different habitats of the Mugu Lagoon estuarine ecosystem. The salt pans have been excluded because they have not been studied. Symbols: 0 = overwhelming predominance, V = very important, I = important, C = common, and P = present. Symbols in front of virgule (/) = before 1978, after virgule = after 1978.

Plants	Sand-channel (always submerged)	Ponds (always submerged)		Tidal flats (submerged at high tides)			Lower marsh (submerged at most higher high tides)	Upper marsh (rarely submerged)
		Sand + mud	Mud	Sand	Sand + mud	Mud		
Phytoplankton[a]	P/P	P/P	/P					
Benthic microflora[b]								
Diatom	V/V	V/V	/V	V/V	V/V	/V	V/V	I/I
Blue-green	P/P	P/C	/I	P/C	P/I	/V	C/V	V/V
Macroalgae[c]								
Enteromorpha	C/C	I/C	/C	C/C	/C	0/I	C/C	
Ulva	/C	C/I	/0	/C	C/C	/I	/C	
Submerged vascular[c]								
Zostera marina	C/C	0/	/C	C/	I/			
Ruppia maritima		I/	/I					
Emergent vascular[d]								
Salicornia virginica							0/0	V/V
Jaumea carnosa							P/P	I/I
Frankenia grandifolia							P/P	C/C
Limonium californicum								C/C
Suaeda californica							P/P	C/C
Batis maritima							P/P	C/C
Monanthochloe littoralis								C/C
Distichlis spicata								P/P
Triglochin concinnum								P/P

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[a] Phytoplankton enter intertidal areas on high tides, maybe even in similar densities to the subtidal areas. However, the contribution of phytoplankton is negligible even in subtidal areas and has to be much smaller than that in intertidal areas, because the water column is present much less of the time. In addition, the entrainment of benthic forms will be great, diminishing still further the proportionate contribution of the phytoplankton.

[b] Green algae also are seen in samples taken from benthic microfloral films and mats across their whole range but are so rare as to be ignored in this account. The trends are based on Wilson (1980) - subtidal channel, microscopic observations; Shaffer (1982) - all subtidal and tidal flat habitats, pigment concentrations and microscopic analyses; Holmes and Mahall (1982) and R.W. Holmes (pers. comm.) - bare areas in the upper marsh, microscopic observations.

[c] Based on unpublished data of C.P. Onuf and G.P. Shaffer: casual before 1978 and systematic determinations of density of cover at monthly intervals or less from 1978 to 1981.

[d] Based on unpublished data of C.P. Onuf: percentage cover and biomass in the autumn of 1976, monthly biomass in 1977, and biomass at time of peak standing crop, 1978-81.

predominated the live material in all water samples collected in the lagoon, irrespective of location and tidal conditions. Even in those samples collected explicitly to reflect the maximal influence of incoming oceanic water (in which the relative importance of phytoplankters presumably would be greatest), benthic diatoms predominated almost to the exclusion of neritic and oceanic taxa (R.W. Holmes, University of California, Santa Barbara; unpubl. observ.). (2) Water samples collected from the same water mass on a rising tide as it entered the lagoon and again 2 h later, after it had entered the first (western) big subtidal pond, showed a sixteenfold increase in cell numbers in the 2 h since entering the lagoon, apparently by the entrainment of benthic forms (M. Huff, University of California, Santa Barbara; unpubl. observ.). (3) In a year-long study involving more than 60 days of field observations, the primary productivity of the water column almost always was negligible in comparison to that of the underlying substrate. Microscopic examination of the rare occasions of high productivity invariably revealed a preponderance of benthic diatoms in the water column (Shaffer 1982).

The structural role of the benthic microflora is remarkably important, at least in the sand channel. Here, where the currents appear too fast for the macrophytes to dominate, the benthic microflora can occupy the sediment surface and grow into a continuous film extending over many meters. This film stabilizes the surface. Only in the tidal inlet and delta is the film's capability to hold the surface exceeded (Warme 1971).

Although benthic diatoms are similar in abundance over a broad range of habitats (Table 3), individual species show more distinct habitat segregation and even within-habitat differences. Wilson (1980) noted a distinct difference in the diatom assemblages of sites in the subtidal channel only 45 m apart in the same general habitat. The sites differed in depth, current velocity (at least at lowest water), and substrate, especially the coarse fraction. Wilson tested the hypothesis that substrate characteristics governed the composition of the benthic diatom community by transplanting sediments between sites, and found that this was not the case. Wilson speculated that the much more variable temperature regime was involved (see Chapter 2), but that remains speculation at this stage.

A strong seasonality is evident in Shaffer and Onuf's (1983) 13 months of data on the biomass of the benthic microflora as measured by the concentration of chlorophyll a in the top 5 mm of sediments (Figure 24). Biomass was high (>20 µg

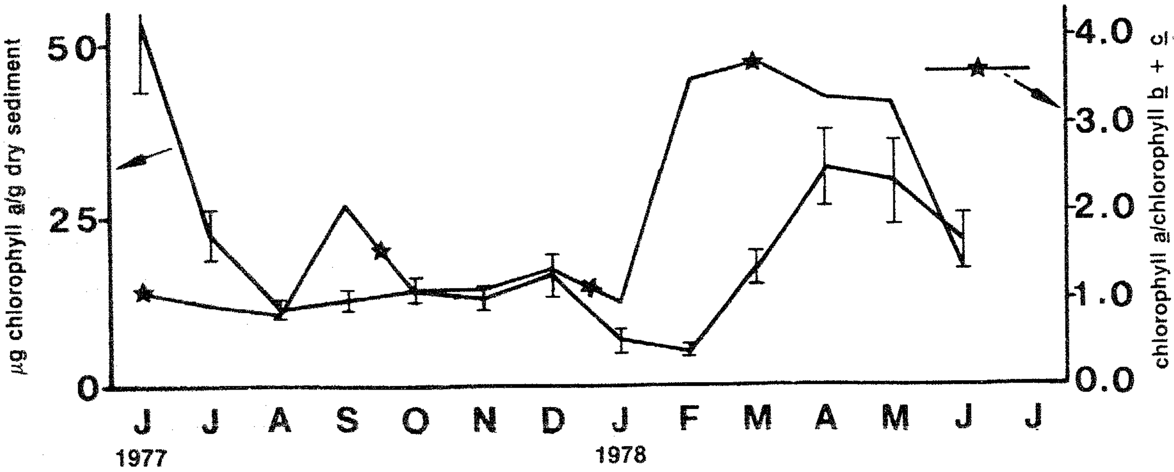

Figure 24. Changes in pigment concentration and composition from June 1977 to June 1978.

chlorophyll a per gram dry weight of sediment) at the beginning of the study in June and July 1977, intermediate and close to constant (10-15 μg/g) August through December, very low (<7 μg/g) in January and February 1978, intermediate again in March, and high April - June. This period was almost evenly split by the February storm that so radically transformed the bottom of the lagoon, so it is not known whether the spring increase is representative of a "normal" year. The winter low is, however, since it was evident in January.

The short sampling period hampers the identification of storm-related effects on the benthic microflora. For June, the only month sampled before and after the February 1978 storm, chlorophyll a was 60% less in 1978 than 1977, suggesting a substantial decline in biomass caused by the storm. However, data for productivity in July, to be discussed in the next chapter, lead to the opposite conclusion. Apparently, the drastic transformation of the bottom of the lagoon from mostly sand to mostly mud did not cause a major change in microfloral biomass. In contrast, an abrupt and persistent change in the spectral characteristics of pigment extracts, interpreted as a change in the ratio of chlorophyll a to chlorophylls b and c, between January and February 1978 indicates a major change in the species composition of the microfloral community (Figure 24). The observed pattern of a great increase in chlorophyll a relative to chlorophylls b and c is consistent with a larger proportionate contribution of Chrysophytes, the blue-green component of the microflora (containing chlorophyll a only) compared to diatoms (containing chlorophylls a and c) and green algae (containing chlorophylls a, b, and c) (Parsons and Takahashi 1973). In turn, this fits well the observations of many others that blue-green algae are most abundant in association with fine sediments (e.g., Rheinheimer 1976).

Prior to 1978 the subtidal parts of the eastern arm were about evenly split between dense meadows of eelgrass and apparently bare bottom covered by a microfloral film very heavily dominated by diatoms. For relatively brief periods in the late spring and autumn, mats of the macroscopic green alga Enteromorpha would grow luxuriantly along much of the shoreline of the subtidal ponds, both on the tidal flats and in the subtidal areas immediately adjacent. Even when drained of water, these mats were several centimeters thick. The reason for ranking the macrophytes even higher than the benthic diatoms in Table 3 is that the macrophytes comprise the entire habitat in the specific situations noted. By virtue of their huge mass and ability to occupy the whole volume of the aquatic habitat, not just its solid surface, their impact probably is considerably greater than that of the microfloral film. Trophically, this may not be the case, although it is difficult to compare the direct grazing pathways originating in the microflora with the indirect-grazing detrital pathways that are so much more important where macrophytes predominate.

After the storm of 1978, cover by macroalgae increased greatly in subtidal areas and remained abundant for much longer periods in intertidal and subtidal zones. In the first year after the storm, Enteromorpha accounted for the great majority of coverage. Since then, Ulva has become increasingly abundant and now predominates overwhelmingly. It is impossible to discount the effects of the major depositions of mud in 1978 and 1980 in bringing about these changes, although the mechanism involved remains unknown.

Through 1977, eelgrass (Zostera marina) occurred in dense beds covering approximately half of the subtidal area in the eastern arm of the lagoon and extending into the lowermost part of the intertidal zone. Although no determinations of biomass and productivity have been made, both must have been large, as attested by the predominance of dead eelgrass in the wrack at the high-tide line and stranded in the marsh (pers. observ.). Eelgrass was a more important determinant of habitat characteristics than the macroalgae, because it was abundant throughout the year and widespread in the lagoon. Changes in eelgrass resulting from the February 1978 storm are relatively easy to interpret. The length of eelgrass varies according to the depth of the water in which the plants grow. On intertidal flats and in the shallowest subtidal areas, blades generally are less than 0.5 m long, whereas in the deepest part of the lagoon, their length usually exceeds 1 m long. The shallow-water plants were completely buried and apparently suffocated. In deeper areas most plants survived the initial inundation, because their greater length insured that most of each plant was well above the bottom all of the time. However, the deep beds thinned gradually over the next several months until they too were extinct by fall 1978. Probably this was the consequence of the normal aging and sloughing off of the blades already in existence when the sediments were deposited, except in this case there was abnormal absence of replacement.

New shoots develop from the thickened basal portion of the plant, ordinarily located at the surface of the sediments. In ten sets of tagged plants that survived the initial burial, shoots continued to develop, only now 10 - 15 cm below the surface (determined by removing the overburden of new sediment from the plants). However, none of the shoots reached the surface, or if they reached the surface, they did not survive the 2 weeks until the next observation (Onuf, unpubl. observ.). Apparently, new shoots cannot penetrate an overburden of 10 cm of anaerobic sediments.

The eelgrass beds have not recovered since. Only a few patches were seen in an aerial survey conducted as recently as September 1986 (R. Dow, U.S. Naval Air Station, Point Mugu, California; pers. comm.).

The Lower Marsh Vegetation

In general, Joy Zedler's monograph The Ecology of Southern California Coastal Salt Marshes: A Community Profile, a companion volume, presents a much fuller account of the emergent marsh than it is possible to assemble from research conducted at Mugu Lagoon. Please consult this valuable source for topics such as zonation and plant-soil relationships, including responses to soil salinity and moisture. Here we confine ourselves to aspects of the distribution of marsh-plant biomass in the eastern arm of Mugu Lagoon that have been studied in detail (Onuf unpubl.). These data may be noteworthy because they are unusual compared to data from other locations.

The most obvious feature of the lower marsh is the virtual monoculture of perennial pickleweed Salicornia virginica (Table 3). This trait is common to all coastal salt marshes from Long Beach to the Golden Gate, apparently with a single exception elsewhere in Mugu Lagoon (Macdonald and Barbour 1974). Cordgrass (Spartina foliosa) was virtually eliminated by dredging in the 1950's and 1960's (Macdonald and Barbour 1974). It is present today in four areas of the lagoon and is expanding in the western arm (R. Dow, pers. comm.). Zedler (1982) noted the association of Spartina with "wetlands with a history of good tidal flushing"; however, this alone is not an adequate explanation for its near absence from the eastern arm.

The biomass of perennial pickleweed is differentiated into succulent green shoots and brown woody supporting stems (Figure 25), the brown stems being the larger fraction throughout the year (Figure 26). Even though the succulent green shoots continuously increased in biomass per square meter between January and June and maintained near maximum biomass through August, there were no detectable changes (by analysis of variance) in total biomass (green + live brown parts) over the course of a year. While this partly reflects the great spatial heterogeneity of the marsh (see next paragraph), it is more an indication of the protracted growing season of southern California and the large allocation of biomass in perennial pickleweed to woody supporting stems. Apparently, the periods of accumulation and death of woody parts overlap so much that net changes cannot be detected during the year, despite the strong seasonality in the biomass of the succulent green growing tips.

Onuf analyzed aspects of the spatial heterogeneity in marsh plant biomass in the marshes fringing the eastern arm of the lagoon. Three features were identified: (1) Marsh plant biomass was as variable on a small scale (decimeters) as on a larger scale (meters), (2) Biomass tended to decrease with distance from the lower edge of the marsh (Figure 27), and (3) Biomass patterns as a function of distance from the mouth of the lagoon changed from year to year from 1978 to 1981.

Figure 25. The dominant plant of the salt marsh, perennial pickleweed (Salicornia virginica), has succulent green shoots year-round, but the woody brown supporting stems always constitute a larger fraction of total biomass.

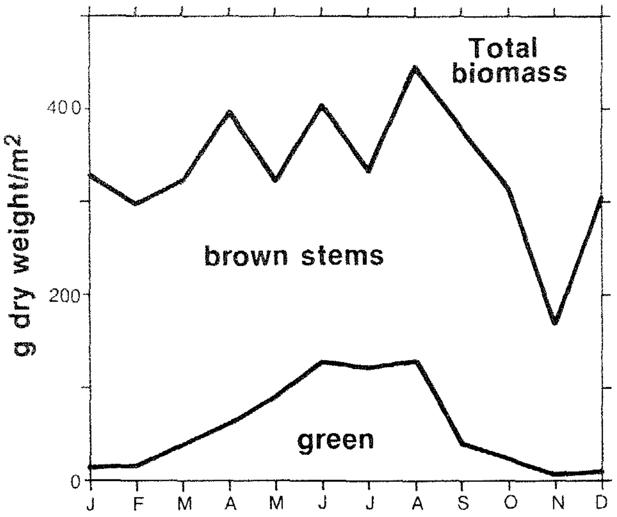

Figure 26. The biomass of Salicornia virginica in the lower marsh at Mugu Lagoon in different months.

Biomass tended to be high near the mouth of the lagoon and much lower far from the mouth in 1978. The strength of this trend progressively weakened in 1979 and 1980 and reversed in 1981, when biomass was lowest near the mouth (Figure 28a). This shift in distributional pattern over time was expressed as a highly significant year x location interaction in analysis of variance, most easily visualized by plotting the location means for each year as linear regressions of biomass vs. distance from the mouth of the lagoon (Figure 28b).

These last results provide information about the effects of major storms on the salt marsh. Onuf et al. (1981a) interpreted the higher biomass of all locations

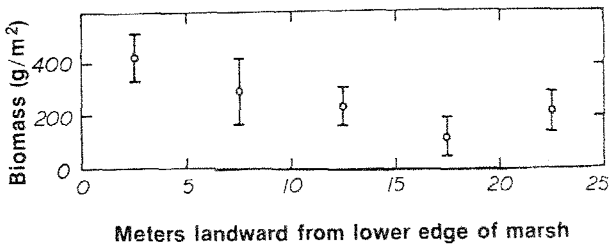

Figure 27. The biomass of Salicornia virginica vs. distance from the lower edge of the marsh. Means and 95% confidence intervals are plotted.

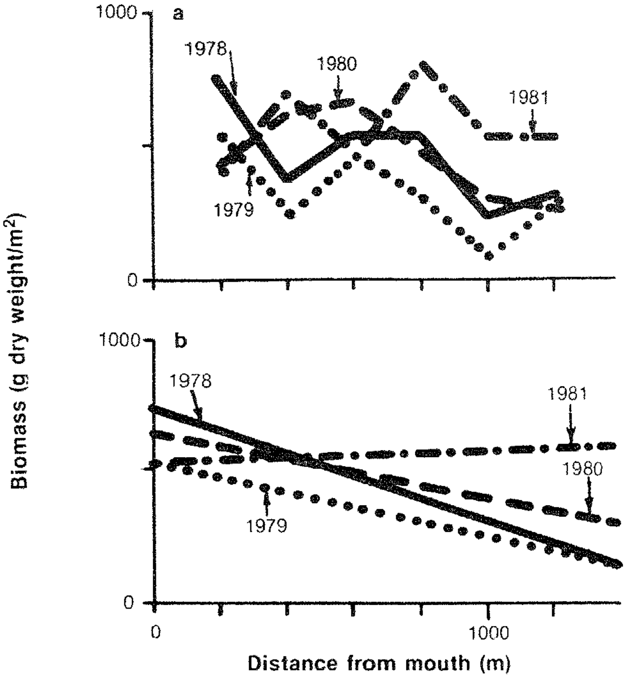

Figure 28. An illustration of the years x location interaction on the biomass of Salicornia virginica in the lower marsh at Mugu Lagoon: (a) means for the six locations progressively farther from the mouth of the lagoon for 1978 through 1981; (b) expressed in the form of linear regressions.

in 1978 over 1979 as a stimulation of growth by the major storm of February 1978, followed by a return to "normal" conditions in 1979. Presumably, the storm stimulated growth either by reducing the salinity of the soil or by adding nutrients via the thin layer of sediments it deposited. This interpretation remained generally tenable in 1980 with its major storm. However, short-term stimulation was not the explanation for the biomass increases seen in 1981, which had no major storm.

Some evidence suggests that the deposition of sediments by storms in the eastern arm may have had opposite effects, depending on the site and its prestorm characteristics. Deposition of new fine sediments on what had been a well-drained, relatively sandy substrate near the mouth apparently made it less suitable for marsh plant growth, whereas deposition on previously waterlogged fine sediments away from the mouth actually made an improvement by raising the marsh surface slightly, thus reducing waterlogging and allowing better aeration of roots (Onuf et al. 1981b). These changes may indicate a mechanism for succession due to storm sediment deposition, an interpretation supported by one other observation: Jaumea carnosa, a high-marsh plant, invaded the low marsh in one location during this study, suggesting an increase in elevation at that site.

The Upper Marsh Vegetation

All information on the upper marsh is from one area located approximately halfway between the mouth and the eastern terminus of the lagoon. Extensive preliminary sampling indicated that this part of the marsh was representative of all of the marsh surrounding the eastern arm of the lagoon in percentage cover of the common species.

Perennial pickleweed is the major contributor to biomass of the upper marsh (Figure 29), but the upper marsh is not a monoculture in the way that the lower marsh is. Based on the overall annual average for ten samples collected each month, perennial pickleweed (Salicornia virginica) accounted for 44% of total biomass; sea lavender (Limonium californicum), 21%; alkali heath (Frankenia grandifolia), 15%; Jaumea carnosa, 14%; saltwort (Batis maritima), 5%; and arrowgrass (Triglochin concinnum), 2%. The two other species that were collected together accounted for less than 1%: sea-blite (Suaeda californica) and annual pickleweed (Salicornia bigelovii). The flora is more diverse than that of the lower marsh but still is relatively simple.

It might be expected that a more varied flora would result in a more even distribution of biomass over the year, since different species would reach peak biomass at different times. This is not evident from Figure 29. The maxima in May and July are twice the minima in January and December, partially because species without overwintering woody parts, Jaumea and Triglochin, are present. The erratic

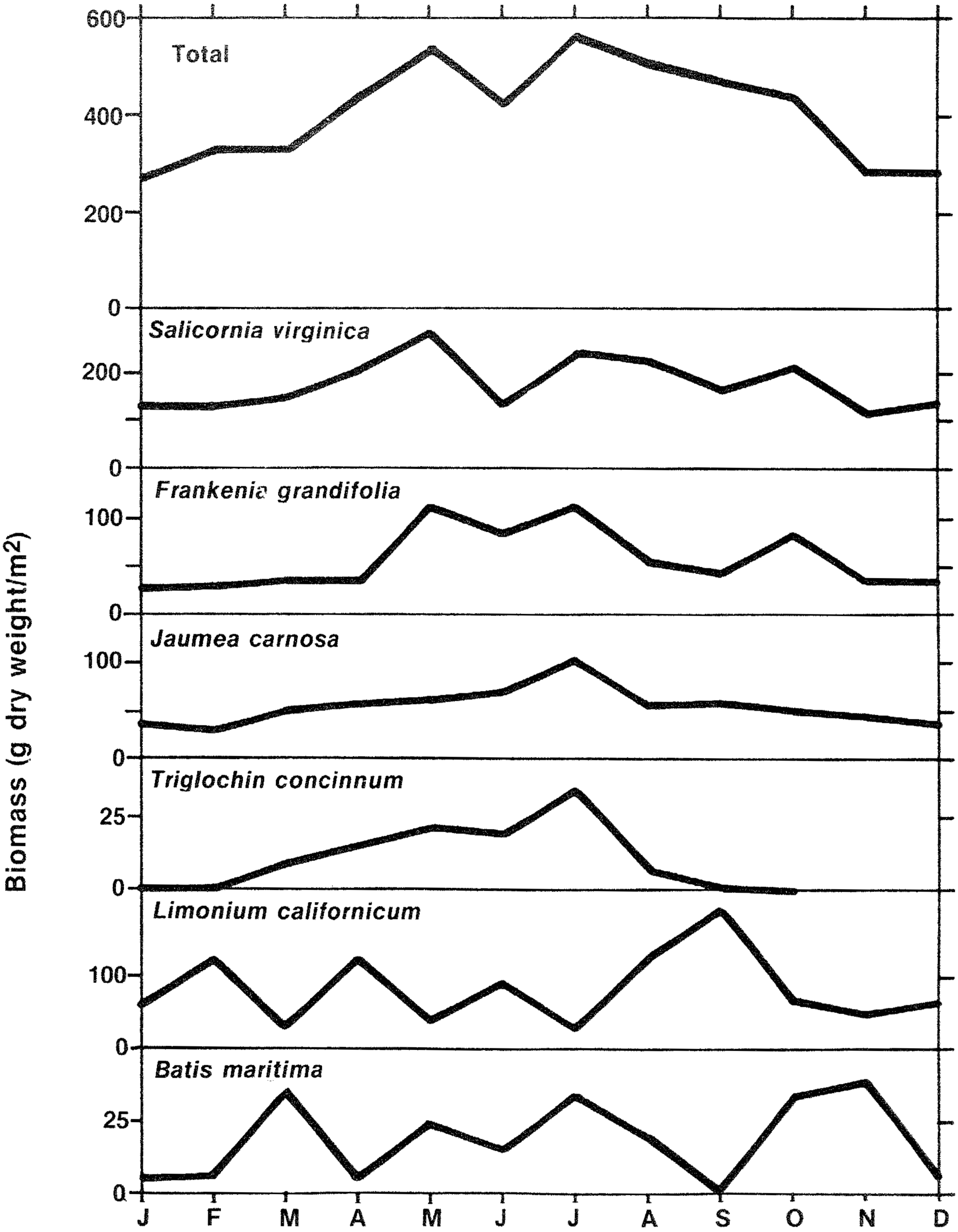

Figure 29. The biomass of common plants of the upper marsh at Mugu Lagoon in different months, 1977, mean of ten 0.06-m^2 samples each month.

fluctuations in most species can be explained by patchiness. The more curious outcome is that Salicornia virginica biomass is more strongly seasonal at this elevation than in the lower marsh, perhaps because of the slightly different allocation of biomass between woody parts and green growing tips. Over the year as a whole, the biomass of woody parts is 4.9 times that of green parts in the lower marsh, as compared to 3.6 in the upper marsh. Thus, the highly seasonal component of perennial pickleweed (the green shoots) is proportionately greater in the upper marsh, but we have no idea why.

In the previous section, year-to-year changes in the biomass of the lower marsh were interpreted in terms of succession in response to sediment deposition. The data base for the upper marsh is only one-third as large and cannot be analyzed to the same extent. The most obvious manifestation of a successional change in the upper marsh would be incremental and differential changes over time in the biomass of different species. There is no striking evidence of this in the 5 years sampled between 1977 and 1981 at the time of peak standing crop (Figure 30). Those species that contributed relatively little to total biomass at the beginning contributed relatively little at the end. Those that contributed the most biomass at the beginning contributed most at the end. Only the contrast between Salicornia and Jaumea suggests incremental changes: the biomass of the former decreased from 1978 to 1981 and the biomass of the latter was almost twice as great from 1979 to 1981 as in 1977 and 1978.

Another way to look at the response of the upper marsh over the long term is to contrast it with the nearby lower marsh. The plots of mean biomass in different years for the upper and lower marsh are virtually mirror images across the overall mean for all years and locations (Figure 31). For the first 3 years, biomass of the upper marsh was higher than the lower marsh, but the opposite was true for the last 2 years.

We have learned much about the distributions of the plants, how they are changing and what the principal driving force of that change is. Unfortunately, we are far

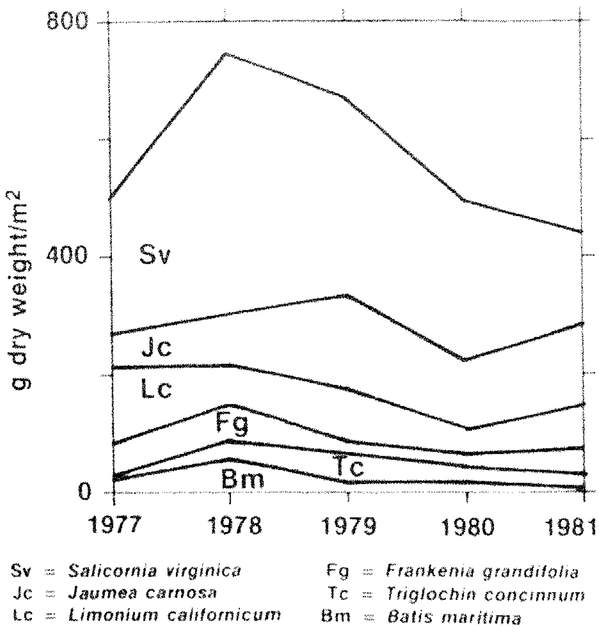

Figure 30. Changes in the biomass of the common plants of the upper marsh at Mugu Lagoon, 1977-81.

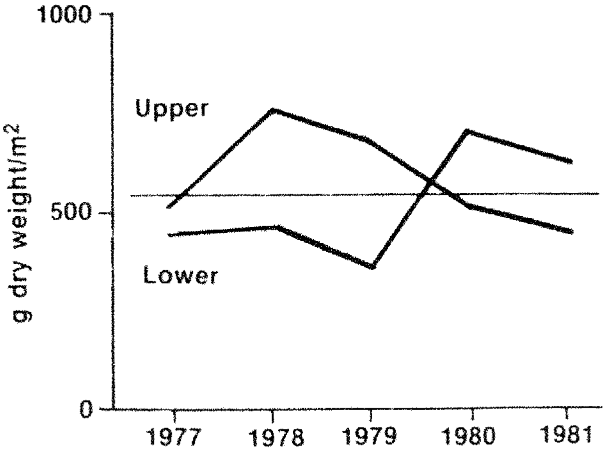

Figure 31. Changes in mean biomass of salt marsh plants in the upper marsh compared to the lower marsh, 1977 to 1981. The horizontal line at 550 g/m² is the overall mean of all sites and years.

from understanding the mechanisms that bring about these changes. Also, we do not know how applicable this description for the eastern arm is to the larger expanse of salt marsh in the western arm. Casual observations indicate that the two areas of marsh are similar floristically, but that the vegetation is denser and taller in the western arm. On a larger scale, the Mugu Lagoon salt marsh differs greatly from the better-known salt marshes of the east and gulf coasts. Instead of dominance by grasses such as Spartina alterniflora, S. patens, and Juncus roemerianus as in the eastern United States, succulent halophytes such as the Salicornias, Jaumea carnosa, Batis martima, and Suaeda californica, and other morphologically complex plants such as Limonium californicum and Frankenia grandiflora prevail. Local and interregional comparisons will be pursued further in Chapter 6.

4.2 THE INVERTEBRATES

There has been no survey of zooplankton, although, like the phytoplankton, they are probably primarily marine species: copepods, cladocerans, ostracods, arrow worms, and planktonic larvae of the benthic invertebrates (Macdonald 1976b). Study of the invertebrates of Mugu Lagoon has been intensive but selective. With the exception of the MacGinities' (1969) brief summary of the biota of the whole lagoon, Wolfe et al.'s (1979) analysis of 12 samples for the western arm, and species lists compiled from 5 areas in and around the central basin in 1980 and 1981 (Soil Conservation Service 1983), reports are limited to the eastern arm. The taxa, preponderance of small species, and high densities (30,000 per m^2) reported by Wolfe et al. (1979) are characteristic of the mudflat environments studied in greater detail by Quammen (1984) in other locations and are consistent with the fine-sediment, low-energy environment attributed to the western arm in Chapter 3, based on superficial observations. In addition, high densities of Tryonia imitator, a small brackish-water gastropod, in the far western end of the western arm are consistent with the prediction in Chapter 2 that freshwater inputs would have their greatest influence there. The sampling of the central basin was sampled after most of the subtidal area had been filled by the major storms of 1978 and 1980 (Figure 14). The large number of insect taxa reported (Soil Conservation Service 1983) indicates a large influence of Calleguas Creek under the present conditions.

Within the eastern arm, macroinvertebrates with hard parts - crustaceans, echinoderms (sand dollars) and especially mollusks - have received a great deal of attention. However, even here, coverage has been uneven. Only Macdonald (1969) sampled within the salt marsh, whereas Warme (1971) sampled most types of tidal flats and to a lesser extent subtidal areas, and Peterson (1975) only sampled the subtidal sand channel. Warme (1971) recognized two major assemblages: "the sand-channel fauna" and "the mud-tolerant fauna" of the inner lagoon. Smith (1981) studied the distribution of ciliated protozoans along the sandspit shore of the eastern arm. Smith (1981) found little evidence of habitat differentiation by protozoans with respect to the environmental gradients that he distinguished along the sandspit, probably because the differences in sediment characteristics, temperature, and salinity between sample sites were small compared to other studies where habitat differentiation was reported. Abundances were comparable to those reported by other workers and were highest in the finest sediments before the major storm of February 1978. After the deposition of large amounts of mud throughout the lagoon, abundances were highest in the coarser sediments near the mouth, presumably because the organic content increased while pore space remained high. Away from the mouth, the organic content increased, but pore space diminished (Smith 1981).

These data are too restricted to serve as the foundation for this chapter. Instead, we base most of the following on our previously unpublished invertebrate data. The advantages are that we sampled all physiographic units except tidal creeks and salt pans (Figure 32a); included the "soft" invertebrates, mainly polychaete and oligochaete worms, phoronids, sipunculids (peanut worms), and holothurians (sea cucumbers), as well as those with hard parts; and spanned the major storms of February 1978 and 1980 for

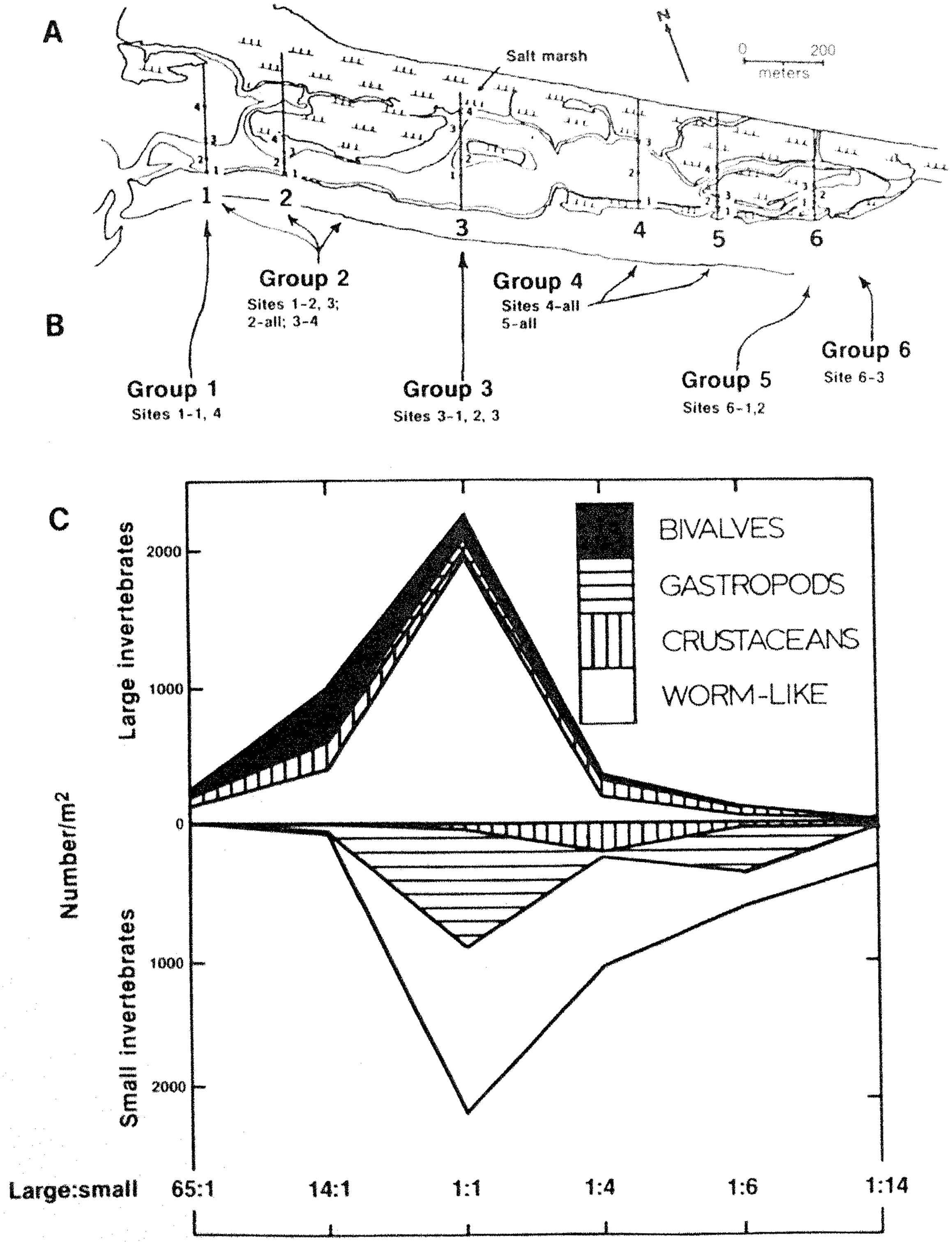

Figure 32. (a) Locations sampled quarterly for invertebrates in the eastern arm of Mugu Lagoon in 1977, (b) sites grouped according to 50% similarity in densities of major categories, and (c) mean densities of those categories in each group.

two areas (Transects 2 and 3, Figure 32a). In subtidal areas and intertidal flats, the samples consisted of all material retained by a 3-mm screen (Transects 1 and 2, the sandy areas) or a 1-mm screen (Transects 3 through 6, the muddier areas) excavated from within a steel cylinder 1/16 m^2 in cross-sectional area to a depth of $\sim$50 cm. Within the marsh only the epifauna were recorded from the 1/16-m^2 samples collected as part of the plant productivity studies. Invertebrate sampling did not address zooplankton and microfauna. Despite these omissions, the similar methodology for all tidal flat and subtidal areas allows comparisons between locations and years for similar kinds of organisms.

Duplicate quarterly samples were combined for each site (Figure 32a), and the average annual density of each taxon was determined. The taxa were grouped into eight morphotype categories: large and small worm-like organisms, large and small gastropods, large and small crustaceans, bivalves (large), and sand dollars (large). Large and small correspond roughly to scales of centimeters and millimeters, respectively, for the largest dimension of the most common size classes of each taxon. Table 4 indicates the

Table 4. Mean density of invertebrates (number/m^2) in 1977 for all sites sampled in the eastern arm of Mugu Lagoon. For Transects 2 & 3 combined, mean densities are reported for 1977 and 1978-80. Indications of responses to storm-caused alterations of the study area are also given. See the text for a description of the sampling procedure and Figure 32 for locations sampled. p = present at <1 per m^2. A taxon had to be present at >5 per m^2 on at least 1 transect in at least 1 year to be listed individually.

		Transects 2 & 3					
Invertebrates	All transects 1977	1977	1978-80	Down all 3 years after storm	Gone	No change	Up
	Mean density (no./m^2)			Population response to storms			
Large Worm-like							
Notomastus tenuis	307	775	330	x			
Haploscoloplos elongatus	58	7	3		x		
Phoronid	47	108	23	x			
Pareurythoe californica	13	25	18			x	
Nemertean	11	13	10			x	
Hemipodus borealis	10	15	4	x			
Goniada sp.	9	23			x		
Nereis sp.	5	14	p	x			
Axiothella rubracincta	5	10			x		
Sipunculid	p	p	9				x
Ophelia	3	5	p	x			
Total	470	999	395	x			
Small Worm-like							
Leptosynapta albicans	350	313			x		
Sabellid sp.	36	96			x		
Spiophanes missionensis	29	45			x		
Oligochaete sp.	25		158	(Large numbers 1 year)			?
Minuspio cirrifera	18			(Never present)			
Capitella capitata	29		85				x
Polydora sp.	10			(Never present)			
Streblospio benedicti	10	10	160	(Large number storm years)			x

(continued)

Table 4. (Concluded).

		Transects 2 & 3					
Invertebrates	All transects 1977	1977	1978-80	Down all 3 years after storm	Gone	No change	Up
	Mean density (no./m^2)			Population response to storms			
Small Worm-like (continued)							
Armandia brevis	7	9	p	x			
Pseudopolydora sp.			302				x
Total	516	479	709				x
Large Gastropods							
Cerithidea californica	5	13	139				x
Bulla gouldiana	14	30	10	x			
Olivella biplicata	2	3		x			
Crepidula onyx	1	4		x			
Total	22	50	151				x
Small Gastropods							
Acteocina spp.	185	371	668				x
Assiminea californica			128				
Total	185	371	796				x
Bivalves							
Cryptomya californica	135	181	75	x			
Macoma nasuta	15	38	32			x	
Protothaca staminea	9	10	15			x	
Nuttallia nuttallii	5	8	p	x			
Diplodonta orbellus	2	7	8			x	
Chione undatella	3	5	p		x		
Florimetis obesa	2	3		x			
Laevicardium substriatum	1	3	1			x	
Macoma secta	p	2	1			x	
Tagelus californianus	p	p	2			x	
Total	175	260	135	x			
Large crustaceans							
Callianassa californiensis	98	123	45	x			
Hemigrapsus oregonensis	13	11	12			x	
Total	112	136	60	x			
Small crustaceans							
Gammaridean amphipod	28	5	15	(Large numbers 1 year)			?
Caprellid amphipod	19	5	240				x
Cumacean	24	p	21				x
Total	74	11	276				x
Sand dollars							
Dendraster excentricus	2	4					
Total	2	4		x			

taxonomic composition of the different categories by listing the dominants of each category.

Sites were grouped based on the criterion of >50% similarity in densities of the different categories of invertebrates (Figure 32b). Three patterns are evident immediately: (1) The groups were separated primarily according to distance from the mouth of the lagoon; intertidal versus subtidal distinctions tended to be less important. (2) Densities were lowest at the ends of the lagoon (Groups 1 and 6) and around an order of magnitude higher in the middle (Groups 3 and 4). (3) The relative importance of large taxa decreased with distance from the mouth. Another pattern cannot be extracted from this analysis but is important, nonetheless: filter feeders dominated the sand channel and deposit feeders dominated the ponds.

Generally, sediment characteristics are considered the best diagnostic characteristic of the associated invertebrate assemblage. According to the 1977 (prestorm) data, the invertebrate fauna is highly differentiated according to location within the eastern arm, yet sediments did not appear to be differentiated to a corresponding degree. Thus, the bottom of the lagoon was sandy in almost every sample collected from subtidal areas and intertidal flats before 1978 (Warme 1966; Shaffer and Onuf 1983; Shaffer and Cermak, unpubl. observ.). Silts and clays approached an equal share with sand in the middle of the ponds, while sand predominated near the invertebrate-sampling sites at either end of the lagoon. Despite the similarity in sediments and the similarities in total density of invertebrates between east and west ends of the eastern arm, these locations diverged more in the relative abundances of different morphotype categories (as indicated by the large invertebrate to small invertebrate abundance ratio, for instance: 65:1 at the west end as compared to 1:14 at the east end; Figure 32c). Obviously, some other factor besides sediment texture is involved. The changes after the storm of 1978 will explain some of this fine discrimination among apparently very similar habitats and the difference between ends of the lagoon.

Figure 33 presents the same kind of treatment of the data by category of invertebrates as Figure 32 but for different years in the same location (sandy-bottom channel and subtidal pond), rather than different locations in the same year. The response of the invertebrates in the sand channel to major but brief episodes of reduced salinity and burial by fine sediments has been a continuing reduction of abundance experienced almost equally by all groups (Figure 33, channel). The sand dollar Dendraster excentricus was an exception. It was eliminated from Mugu Lagoon by the storm in 1978. Although small individuals were seen occasionally afterwards through 1980, they were not found in any samples. By the end of 1982, large-sized Dendraster again were abundant in the sand channel, only to be eliminated once again during a period of heavy rains in January 1983.

The responses of the invertebrates to the long-lasting alteration to fine sediments in the westernmost pond of the eastern arm were similar to changes in the sand channel only in the persistent reduction of the large worm-like organisms (Figure 33, pond). Otherwise, the responses were large changes in the relative abundances of different categories of invertebrates before and after the February 1978 storm (in which smaller invertebrates generally were favored) and great annual variability after the storm.

The responses of individual species provide more insight into these large-scale patterns and fluctuations (Table 4). The small worm-like invertebrates responded most strongly to the transformation of the bottom. Three species that accounted for 97% of all individuals collected on Transects 2 and 3 in 1977 were eliminated and have not been collected since: Leptosynapta albicans (a holothurian), Spiophanes missionensis, and an unidentified sabellid polychaete. In their place appeared three other species which were not collected in 1977. These three species accounted for 77% of all individuals collected from 1978 to 1980: Pseudopolydora paucibranchiata and Capitella capitata, both polychaetes, and an unidentified species of oligochaete. Pseudopolydora was not collected anywhere in the lagoon in 1977; however, the others

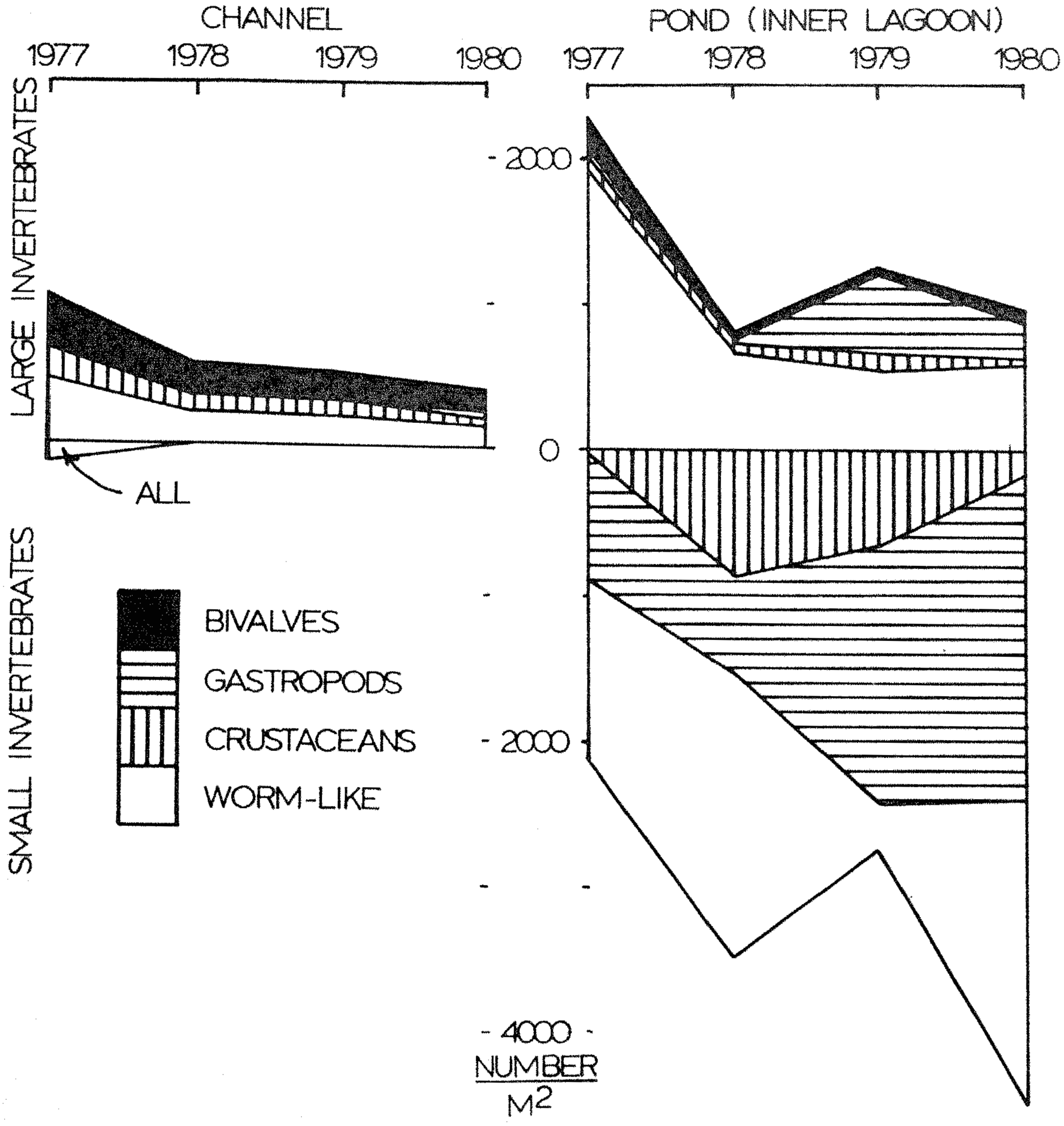

Figure 33. Changes in densities of invertebrates from 1977 to 1980. Sites have been grouped by the criterion of 50% similarity in the densities of the indicated categories.

had been common at one or two sites near the eastern end of the big pond (Transect 4). Streblospio benedicti, a polychaete, was the only species present in the area in 1977 that was much more abundant after the storms, especially in the storm years of 1978 and 1980.

In the other categories of small invertebrates, taxa already present or abundant in the area became more abundant. The small gastropods (Acteocina spp.) almost doubled in numbers. Numbers of various small crustacean species have been large but highly variable among different sites and in different years.

The most abundant large invertebrates exhibited yet another response. They decreased in absolute abundance, but they changed little in relative abundance. Dominant species remained dominant after the storm.

Two factors seem to be most important for interpreting these responses. First, the infaunal elements that inhabited the lagoon in 1977 were affected adversely to a greater extent than epifaunal elements. Second, small invertebrates responded more strongly, whether positively or negatively, than large invertebrates. These infaunal-epifaunal and large-small distinctions appear to be much more informative than faunal-site associations in interpreting the responses of the invertebrates to the storm-caused alterations of the lagoon. Our general expectation was that those taxa most closely allied with the muddiest habitats in 1977 would become more widespread and abundant after the transformation of most of the lagoon to muddier conditions. Conversely, we expected the taxa most closely allied with the sandiest habitats in 1977 to suffer most, perhaps then recovering rapidly only in the sand channel. Instead, the most prominent of the muddy associates disappeared and were replaced, and the most prominent of the sandy associates have doggedly persisted, even in the area that is very muddy now. For example, the polychaete Haploscoloplos elongatus and the holothurian Leptosynapta albicans strongly dominated the large and small worm-like categories, respectively, at the muddiest site in the lagoon in 1977 (Site 2, Transect 4, Figure 32). Both were present on Transect 3 then. Neither was collected in 1979 or 1980. On the other hand, Notomastus tenuis, the dominant large polychaete both in sandy areas and on Transect 3 in 1977, survived in both places, as did the ghost shrimp (Callianassa californiensis) and its commensal clam in sandy areas, Cryptomya californica.

Among some species of low or intermediate abundance, differences before and after February 1978 were consistent with differences in preference of muddy conditions inferred from distributions in 1977. Thus, the bamboo worm (Axiothella rubracincta) was collected almost exclusively in the sand channel in 1977 and was not collected afterwards. The clam Nuttallia nuttallii, only seen in the sand channel in 1977, was not collected at all from 1978 to 1980. The clams Macoma nasuta and Protothaca staminea were relatively abundant in muddy areas in 1977 and did not decline. However, there were counterexamples: the "mud intolerant" clam Diplodonta orbellus of Warme's (1971) analysis did not decline (refuting mud intolerance), nor did the polychaete Pareurythoe californica previously found exclusively in the sandy-bottom channel. Other species associated primarily with muddier areas did decline or disappear: the clam Chione (two species) and the polychaetes Goniada sp. and Nereis sp.

There is a simple explanation for at least part of this counterintuitive result. As illustrated in the previous chapter, no place in the lagoon was truly a mud bottom in 1977; i.e., sand predominated at all stations sampled. Since 1978, the mud fraction has become as predominant as the sand fraction was before 1978. Apparently, the new fine substrate was as novel and foreign for the preexisting fauna of the ponds as it was for the fauna of the sand channel. The sedimentation probably affected the pond fauna more because it lasted longer or affected those organisms more directly. For instance, the anaerobic layer probably lay much closer to the surface after the fine sediments were deposited. This would be much more stressful for a very small organism that relied on gas exchange with interstitial water than for a large organism like the ghost shrimp Callianassa, which pumps large amounts of water from above the sediment surface through its burrows.

The effects of the storm also provide a partial answer to the question posed earlier of why such a narrow gradient of sediment types could yield such a highly differentiated assemblage of invertebrates. The relatively uniform sediment types in 1977 were a reflection of a uniform sediment source, not a monotonous depositional or hydrodynamic regime. When sediments that could be differentiated finally were supplied in 1978, they were differentially distributed (Figure 15). Obviously, the invertebrate biota had been responding to the varied hydrodynamic regime, rather than to differences in sediments. Now, there is a broad spectrum of sediments as well as depositional regimes.

The salt marsh is an unimportant habitat for invertebrates relative to the adjacent tidal flats and subtidal areas; however, a few species can be abundant in some places. They are the gastropod Cerithidea californica and the crab Pachygrapsus crassipes in the lower marsh, and the gastropod Melampus olivaceus in the upper marsh. Melampus is much smaller and probably less abundant than Cerithidea. Macdonald (1969) reported another gastropod, Assiminea californica, to be much more abundant than Cerithidea. We saw large numbers of Assiminea in the lagoon in 1980 but few in the salt marsh at any time. Pachygrapsus occupies burrows in the marsh but is very active on the tidal flats east of Transect 3 (Figure 32) at low tides from April to September. Cerithidea has been abundant in the marsh at Transect 3 throughout our study. Since 1978 it has expanded onto the mudflats on Transect 3, became progressively more abundant 1978 through 1980 at the marsh plant sampling site halfway between Transects 3 and 4, and appeared in the marsh at Transect 4 in 1979 and 1980.

4.3 THE FISHES

Thirty-nine species of fish have been identified from Mugu Lagoon; half the species are common (MacGinitie and MacGinitie 1969; Baker 1976; Onuf et al. 1979; Onuf and Quammen 1983). Only MacGinitie and MacGinitie (1969) and Baker (1976) sampled the three major divisions of the lagoon. Both sources reported fish as least abundant in the western arm and attributed this rarity to the severe restriction of tidal exchange in this part of the lagoon. "Rare or accidental marine species" (Baker 1976) were mostly in the central basin, as might be expected for strays from open-coast habitats, because of the location of the mouth and the prevalence of deep, open water in the central basin when these observations were made (i.e., before 1978).

The four most common species in the lagoon are all small: arrow gobies (Clevelandia ios) inhabit the burrows of crabs and ghost shrimp; topsmelt (Atherinops affinis), occur in dense schools in the water column; staghorn sculpin (Leptocottus armatus) rest on the bottom most of the time; and shiner surfperch (Cymatogaster aggregata) are in dense schools in Zostera beds. The arrow goby, topsmelt, and staghorn sculpin are widespread in the lagoon and can be found all year, whereas the shiner surfperch is localized in its occurrence and highly seasonal. Sharks, rays, and the shovelnose guitarfish (Rhinobatos productus), all elasmobranchs, are the only fish common in the lagoon as large individuals.

More detailed information is available on fish using the eastern arm of Mugu Lagoon (Onuf and Quammen 1983). We sampled the fishes of the eastern arm of Mugu Lagoon by beach seine monthly at four sites from February 1977 to February 1982. We selected the sites to represent the range of major habitats available to fish and to contrast physiographic and vegetational features (Figure 34): shallow (Sites 1 and 2) vs. deep (Sites 3 and 4), and vegetated (Sites 2 and 3) vs. bare (Sites 1 and 4). There also was a gradient in sediment texture: fine fraction increased from Site 1 to Site 4. These sites encompassed most of the range of environmental conditions that might influence the kinds and abundances of fishes present. Habitat types not sampled included marsh channels, the marsh itself, and the shallow subtidal area at the extreme eastern end of the lagoon which differs from the shallow sites that we sampled by having almost no tidal current.

Thirty-five species were caught in the first year of sampling. Two species, topsmelt (Atherinops affinis) and shiner surfperch (Cymatogaster aggregata) accounted for over three-quarters of all individuals caught. The eight most common

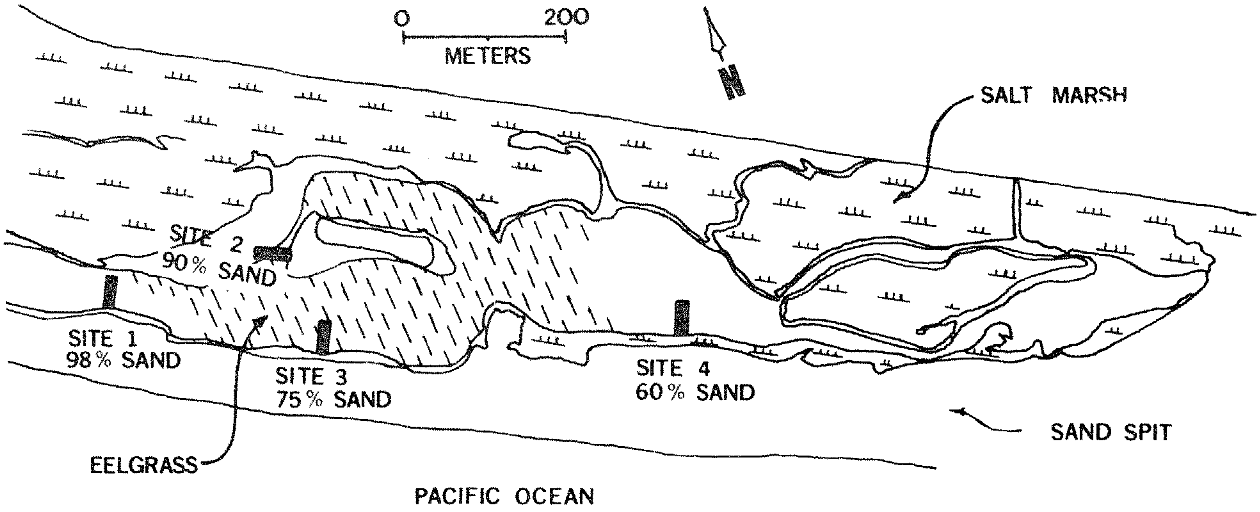

Figure 34. Fish-sampling sites and their characteristics in 1977.

species accounted for 96% of all individuals caught. Data from the 9 months when all stations were sampled indicate that depth and cover by eelgrass were equally important as determinants of fish abundance. Catches were least in the shallow bare site; more than twice as great at the shallow, eelgrass, and deep bare sites, and more than twice as great again in the deep, eelgrass site (Table 5). Apparently, depth and cover by eelgrass interact synergistically for a number of species, since the difference in total species between eelgrass and bare sediment was much greater at the deeper sites than the shallow ones: 23 vs. 15 as compared to 12 vs. 11, respectively. It cannot be determined from these data whether the differences in substrates between sites (Figure 34) contribute to the observed pattern.

All the common species were found at all the sites; however, seven of the eight species making up 98% of the total catch were caught at least 75% of the time at either one or two sites (Table 6). The species were relatively evenly distributed among categories of habitats: three single site associations, each with a different site, and four associations with a pair of sites, each with a different pair. The most common species - topsmelt and shiner surfperch - were found at the deep stations, the surfperch at the vegetated station and the topsmelt at both the bare and vegetated deep stations. Fish caught more often in the shallows included the longjaw mudsucker, the California killifish, and the bay pipefish.

A strong seasonality is evident in the 5-year averages of total monthly catches and for catches of individual species (Figure 35). Most have been caught in every month of the year, but many were very rare at least for a couple of the winter months. The June peak in total catch was not the result of the abundant species behaving similarly, but rather represents large numbers of the two dominant species, topsmelt and shiner surfperch, being present at the same time.

For the species in general, the overriding impression is that the peaks in abundance of individual species were remarkably spread out over the year: essentially two peaks per month from April to October (Figure 35). Perhaps this is an indication that the resources of the lagoon are being partitioned temporally as well as spatially. Alternatively, it may reflect only differences in the temperature preferences of the different species.

Although nearshore fisheries are variable with respect to time (hours, days, months, and years) and place, three factors allowed us to rigorously analyze the

Table 5. Total catch of fishes by species and site in the 9 months of 1977 when all sites were sampled. The percentage contribution of each species to the total at all sites is also shown at the far right. Common names follow Miller and Lea (1972).

Species		Site characteristics				
		Shallow		Deep		
Common name	Scientific name	Bare (Site 1)	Eelgrass (Site 2)	Bare (Site 4)	Eelgrass (Site 3)	%
Topsmelt	*Atherinops affinis*	235	308	738	1,330	48
Shiner surfperch	*Cymatogaster aggregata*	57	216	28	1,197	27
Staghorn sculpin	*Leptocottus armatus*	59	172	249	31	9
California killifish	*Fundulus parvipinnis*	58	121	18	21	4
Diamond turbot	*Hypsopsetta guttulata*	25	47	60	15	3
Bay pipefish	*Syngnathus leptorhynchus*	17	66	13	43	3
California halibut	*Paralichthys californicus*	9	13	104	8	3
Longjaw mudsucker	*Gillichthys mirabilis*	2	65	13	1	1
Bay blenny	*Hypsoblennius gentilis*	1	14		4	
California tonguefish	*Symphurus atricauda*		3	9	6	<1
Giant kelpfish	*Heterostichus rostratus*				18	
Kelp bass	*Paralabrax clathratus*				13	
Brown rockfish	*Sebastes auriculatus*			9		
Opaleye	*Girella nigricans*		7			
Shovelnose guitarfish	*Rhinobatos productus*	1		5		
Grey smoothhound	*Mustelus californicus*			3	3	
Black surfperch	*Embiotoca jacksoni*	1	1		3	
Kelp rockfish	*Sebastes atrovirens*				5	
Barred surfperch	*Amphistichus argenteus*				2	
Pacific herring	*Clupea harengus*			2		
Kelpfish 2					2	
Kelpfish 3					2	
Round stingray	*Urolophus halleri*			1		
Speckled sanddab	*Citharichthys stigmaeus*				1	
Barred sand bass	*Paralabrax nebulifer*				1	
Striped mullet	*Mugil cephalus*			1		
Starry flounder	*Platichthys stellatus*			1		
Spotted turbot	*Pleuronichthys ritteri*				1	
Leopard shark	*Triakis semifasciata*				1	
Total individuals (all stations = 5,460)		465	1,033	1,245	2,717	
%		9	19	23	50	
Total species (all stations = 29)		11	12	15	23	

effects of the major storms of 1978 and 1980 (Onuf and Quammen 1983). First, sampling at the same site monthly for 5 years was frequent enough to identify systematic differences between years by non-parametric statistical procedures, even when the high seasonality and aggregated distributions of the fishes made standard parametric statistics inappropriate. Second, the storms affected the four sites differentially, some much more severely than others. This allowed tests of the following sort: if differences between years were the result of the storms, then bigger changes should be associated with the more severely affected

Table 6. Habitat characteristics of the common species of fishes in Mugu Lagoon inferred from features of the sites at which they were caught most frequently.

	Shallow		Deep	
	Bare (Site 1)	Eelgrass (Site 2)	Bare (Site 4)	Eelgrass (Site 3)
>75% caught at one site				
Shiner surfperch				x
California halibut			x	
Longjaw mudsucker		x		
>75% caught at two sites				
Topsmelt			x	x
Staghorn sculpin		x		x
California killifish	x	x		
Bay pipefish		x		x

sites. Third, the symmetrical sequence of minor and major storm years for the 5 years of sampling (minor-major-minor-major-minor) from February 1977 to February 1982 permitted the strongest possible inferences about the effects of storms. Not only was there replication of the basic comparison between the years immediately following major storms and years at least 1 year removed from major storms, but also there was the opportunity to discriminate between short-term effects (comparisons between adjacent years) and persistent effects (comparisons between sequential storm years or nonstorm years). The analysis is beyond the scope of the profile and is reported in Onuf and Quammen (1983), but the conclusions were straightforward.

All significant differences between years indicated storm-caused declines in the total catch for the whole lagoon and in the total number of species caught in the eastern arm as a whole. Part of the reductions were short term, since increases invariably ensued after each major storm year (Figure 36); however, part of the reductions were persistent, and overall there were almost 50% fewer fish in 1981 than 1977.

The decrease in depth and virtual elimination of eelgrass at all sites within the pond had a cascading effect on the suitability of different sites for different species. The originally shallow, half-eelgrass, half-bare Site 2 became almost entirely intertidal and bare. The originally deep, bare Site 4 became mostly shallow. The originally deep eelgrass Site 3 became bare and shallower, but still was deep in relation to other sites. The originally shallow, almost entirely bare Site 1 did not change in depth but substantially increased in eelgrass cover. Species switched locations accordingly, and those for which no analog of their favored habitat existed at the end of the study declined in abundance (Figure 37). The deep-water habitats of the original dominant species - topsmelt and shiner surfperch - were eliminated. Topsmelt (79% caught at the two deep sites in the first year) were down 57% in the fifth year compared to the first, and shiner surfperch (80% caught at the deep eelgrass site in the first year) were down 97% from the first year to the fifth. Our initial expectation was that species that spent most of their time on the bottom would respond very strongly to the new, fine-textured bottom. We expected those species (California halibut, diamond turbot, staghorn sculpin) associated with Site 4, the muddiest area during the first year, to prosper, and those associated with a much sandier area (California

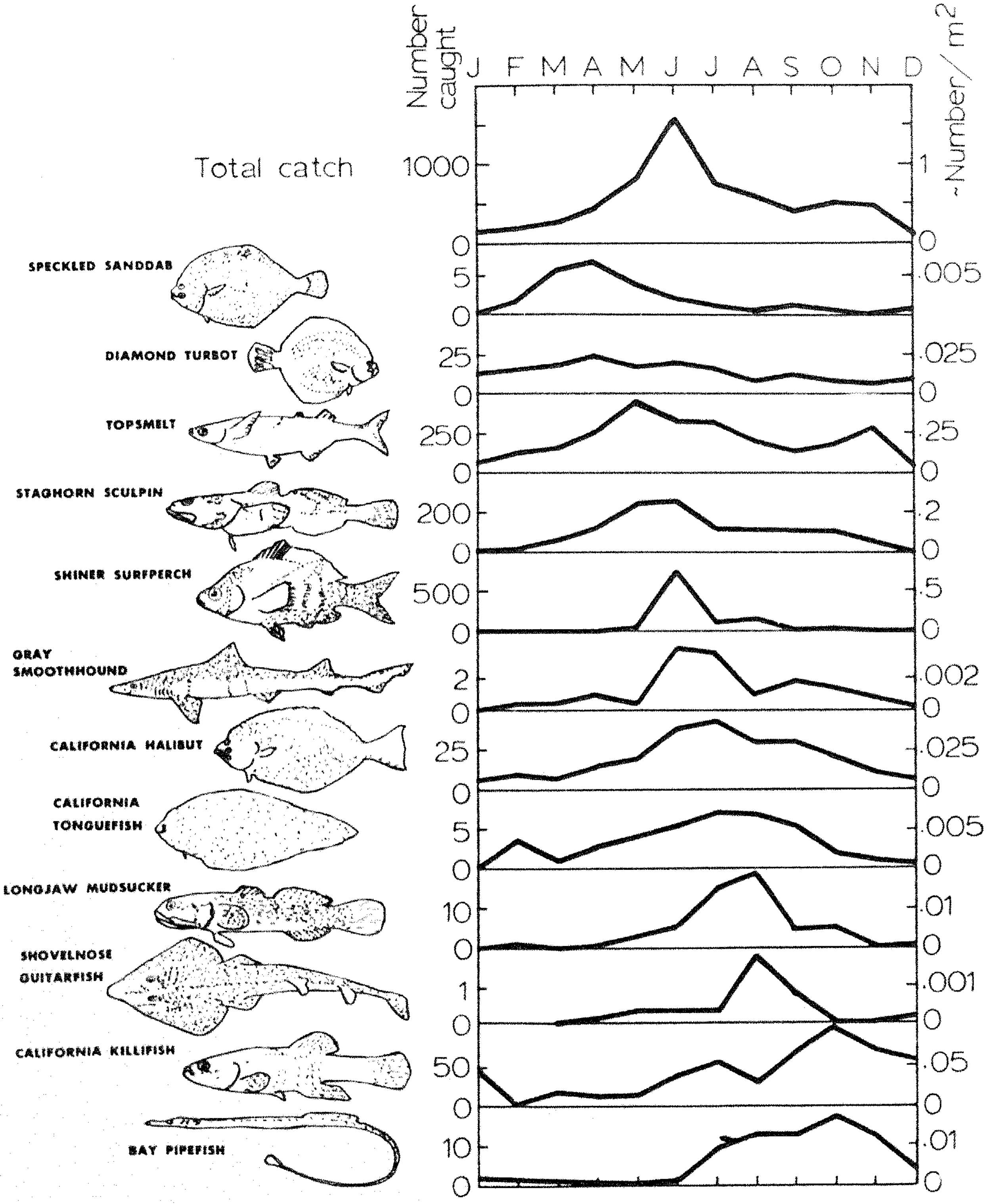

Figure 35. The 5-year average monthly fish catch at Mugu Lagoon, arranged by month of peak abundance, from earliest at top to latest at bottom.

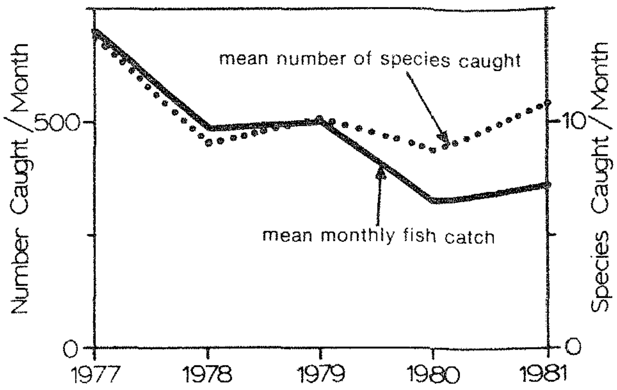

Figure 36. Changes in mean monthly fish catch and mean number of species caught from 1977 to 1981.

killifish, longjaw mudsucker) to suffer. If sediment type had any role in determining numbers and distribution, it was overwhelmed by the effects of depth and cover by eelgrass.

4.4 THE BIRDS

No quantitative bird census data have been published for Mugu Lagoon. The Natural Resources Management Office, Pt. Mugu Naval Air Station, CA, has compiled a list of 198 species found on the Air Station in both wetland and upland habitats (unpubl.). The following analysis of the distribution and abundance of water-related birds in space and time is based on censuses of 21 areas conducted at 20-day intervals near the predicted time of the daylight low tide from October 1977 to September 1982 (Quammen and Onuf, unpubl. data). Census areas were limited to permanent open water and intertidal flats and were located in the western arm and central basin, as well as in the eastern arm.

An average of 2,700 birds was counted per census (Table 7). In all, 73 species were seen during the study; 8 species were observed at more than 100 per census and accounted for more than 70% of the total; and 16 were observed less than once in 10 censuses. The generally small, surface-feeding shorebirds were the most abundant category (33%); followed by coots (16%); diving ducks (mainly mollusk eaters, 15%); large, long-billed shorebirds (probing feeders, 13%); gulls (11%); wading, diving, and aerial fishing birds (6%); and dabbling ducks and geese, (mainly plant-eaters 5%). The category "other" contained mostly strays plus the American bittern (seen mainly in the marsh, feeding on insects), killdeer (seen mainly supratidally on the sandspit shore of the lagoon, feeding on insects), and Northern phalarope, a shorebird relative that feeds on plankton.

There is a strong seasonality in the total abundance of birds in Mugu Lagoon, as indicated by the monthly averages for Sites 1 through 20 (Figure 38). In May and June, 100 to just over 200 birds were counted per census. From July through September, numbers were close to 1,000 and from October through April were between 2,000 and 4,000. December, January, and February were the months of highest abundances, yet only coots and diving ducks reached their maxima in this period. Apparently, Mugu Lagoon is a southern terminus and overwintering area for these migrants. The fish-eating birds showed spring or fall peaks, and in the extreme case of the aerial fishers, had their lowest numbers in the winter. This is consistent with the much higher abundances of fish in the spring and fall (Figure 35). The wading and diving fishers, however, go elsewhere in the summer when fish are most abundant.

The remaining groups had varied seasonal patterns. The probing shorebirds were most abundant in winter and least abundant in May and June, but varied less over the whole year than any other category. The relatively high numbers of surface-feeding shorebirds and dabblers present in midwinter suggest that some overwinter in Mugu Lagoon; on the other hand, the appearance of some in early autumn and greatest abundance in March or April indicate that others migrate through to overwinter farther south. The fall-spring asymmetry of abundance suggests that the southward migration is much less synchronous than the return north as has been noted for some of these species by Recher (1966) and Page et al. (1979).

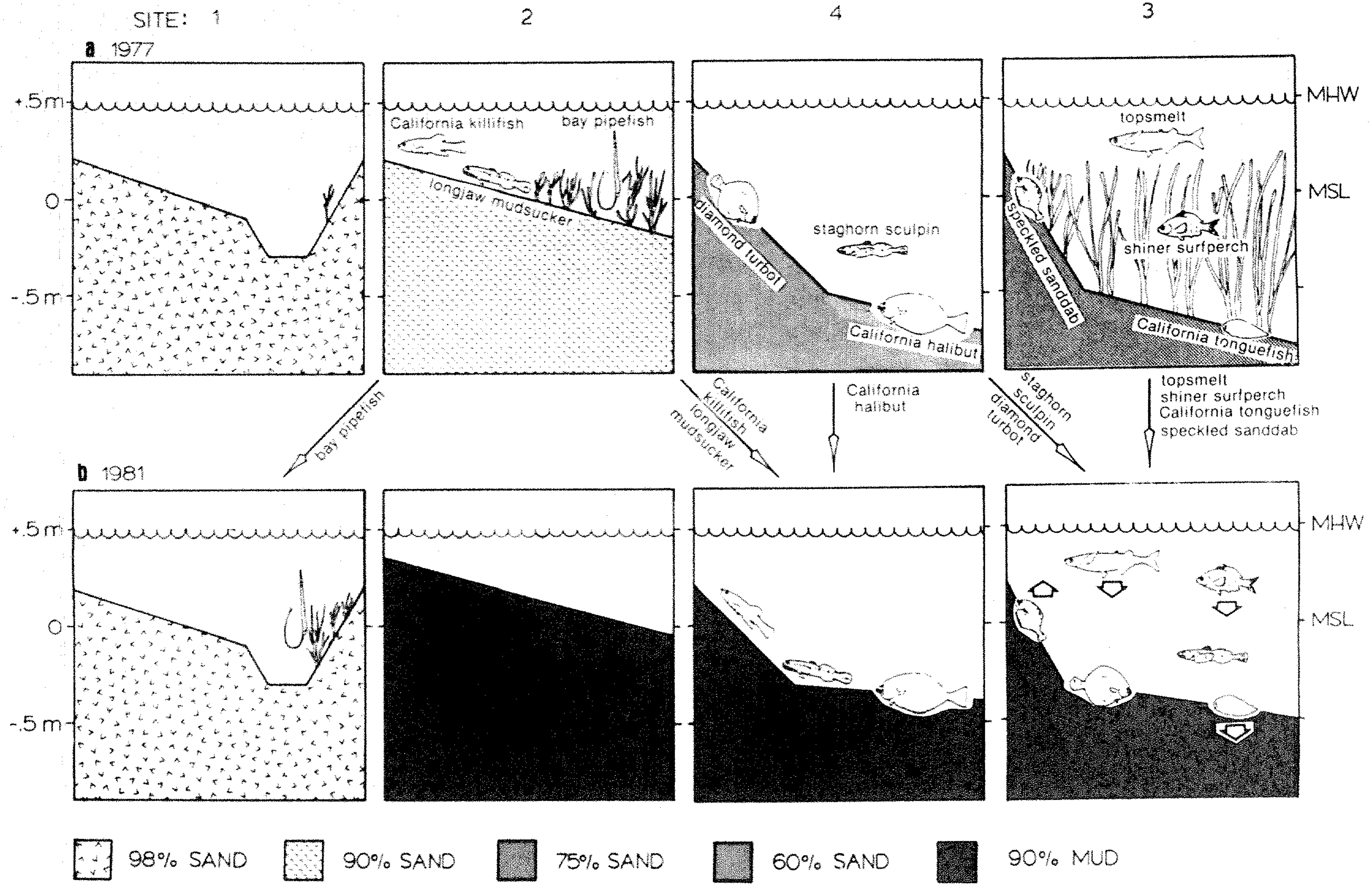

Figure 37. The characteristics of sampling sites and the locations where different species of fish were most commonly caught in 1977 and in 1981. Significantly higher abundance in 1981 than 1977 (⇧), lower (⇩).

Table 7. Abundance ranking and mean number of birds seen per census averaged over all seasons, 1977-82, for 21 census sites (see Figure 39) in Mugu Lagoon. Abundances are given by species and functional category; species are listed in decreasing order of abundance within a category. Rank and site where most commonly observed are also listed.

Rank in abundance			Number seen per census	Site where most often seen
Category	Species			
1		SURFACE-FEEDING SHOREBIRDS	901.7	
	2	Dowitchers spp.	254.4	16
	3	Western sandpiper	245.2	16
	7	Sandpipers[a]	144.6	21
	8	American avocet	140.8	16
	13	Dunlin	44.0	16
	21	Least sandpiper	27.3	16
	22	Sanderling	24.7	21
	28	Black-bellied plover	15.8	21
	36	Stilt	6.6	18
	39	Semipalmated plover	4.6	16
	47	Snowy plover	1.3	5
	52.5	Red knot	0.6	
	57.5	Wilson's plover	0.2	
		Black turnstone	<0.1[b]	
		Ruddy turnstone		
		Surfbird		
		Wandering tattler		
4		PROBING SHOREBIRDS	354.4	
	5	Marbled godwit	200.8	21
	9	Willet	140.5	16
	33	Long-billed curlew	9.3	8
	42.5	Greater yellowlegs	2.2	16
	54	Whimbrel	0.6	
2	1	COOTS	428.0	19
6		DABBLING DUCKS & GEESE	153.6	
	10	Northern shoveler	78.3	21
	18	Northern pintail	28.8	21
	19	American wigeon	28.6	7
	31	Cinnamon teal	9.8	19
	37	Green-winged teal	6.2	19
	50	Mallard	0.8	
	52.5	Canada goose	0.6	
	55	Brant	0.4	
		Gadwall	<0.1[b]	
3		DIVING DUCKS	406.0	
	4	Ruddy duck	237.0	15
	11	Surf scoter	69.2	21

(continued)

Table 7. (Continued).

Rank in abundance			Number seen per census	Site where most often seen
Category	Species			
		DIVING DUCKS (continued)		
	15	Canvasback	40.4	21
	16	Greater scaup	36.7	4
	27	White-winged scoter	16.0	13
	35	Bufflehead	6.7	4
		Redhead	< 0.1[b]	
		Goldeneye		
9		WADING FISHERS	10.3	
	34	Snowy egret	6.9	11
	41	Great blue heron	2.4	21
	48	Great egret	1.0	19
8		DIVING FISHERS	54.7	
	24	Western grebe	19.4	12
	25	Double-crested cormorant	17.7	21
	30	Red-brested merganser	10.6	21
	40	Eared grebe	4.3	4
	46	Pied-billed grebe	1.4	20
	49	Horned grebe	0.9	
	56	Common loon	0.4	
	57.5	White pelican	0.2	
		Arctic loon	< 0.1[b]	
		Red-throated loon		
7		AERIAL FISHERS	109.8	
	14	Brown pelican	41.0	21
	20	Forster's tern	28.3	21
	23	Caspian tern	23.4	21
	29	Royal tern	13.6	21
	44	Elegant tern	1.8	10
	45	Least tern	1.4	13
	59	Belted kingfisher	0.1	
5		GULLS	303.5	
	6	Ring-billed gull	167.8	21
	12	California gull	66.7	21
	17	Western gull	36.2	21
	26	Heermann's gull	17.2	21
	32	Bonaparte gull	9.4	11
	38	Gulls[a]	6.2	21
		Glaucous-winged gull	< 0.1[b]	
10		OTHER	3.0	
	42.5	Northern phalarope	2.2	11
	51	Killdeer	0.8	
		American bittern	< 0.1[b]	
		Emperor goose		

(continued)

Table 7. (Concluded).

Rank in abundance		Number seen per census	Site where most often seen
Category	Species		
	OTHER (continued)		
	White-faced ibis	<0.1[b]	
	Black oystercatcher		
	Flamingo (sp.?)		
	Roseate spoonbill		

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[a] Seen from too far away to identify the species.
[b] Species seen <0.1 per census not ranked.

Bird abundance varied among sites depending on functional category, yet we have been largely unsuccessful in explaining the abundance patterns based on site characteristics. Instead, we turned the process around here, as with the invertebrates. Groups of sites were defined by >60% similarity in their densities of the categories of birds designated in Table 7. Then characteristics of sites were sought that were shared in common within the group but differed from other groups.

The census sites formed six distinct groups according to the criterion of >60% similarity in the densities of ten categories of birds (Figure 39; Table 7).

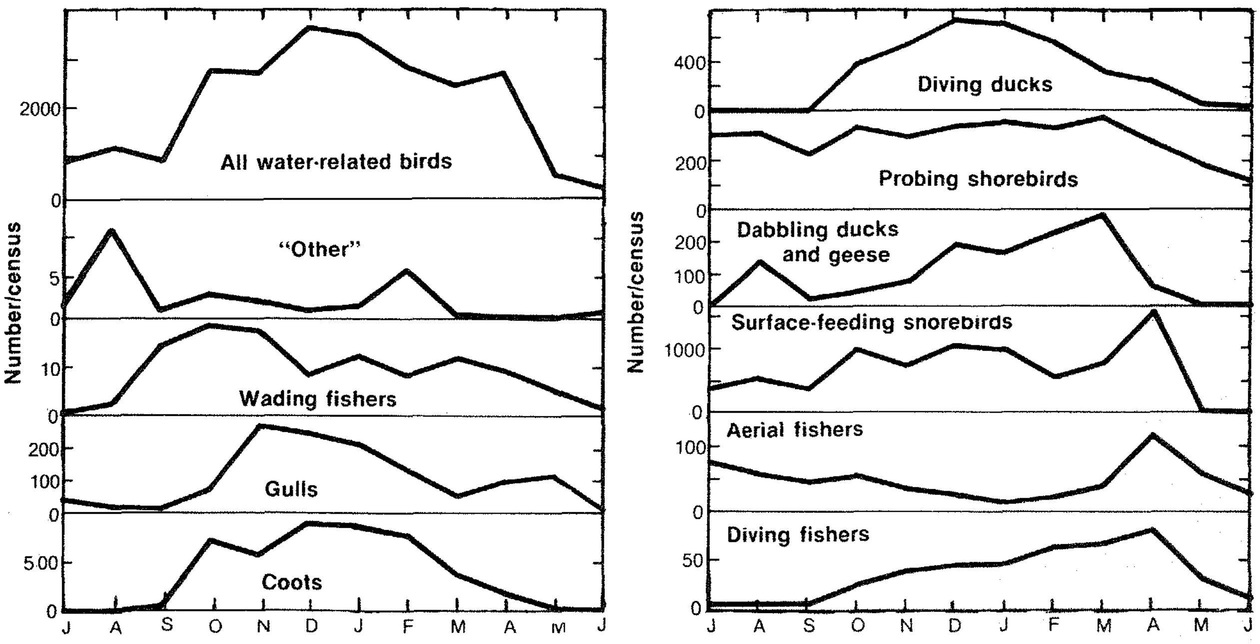
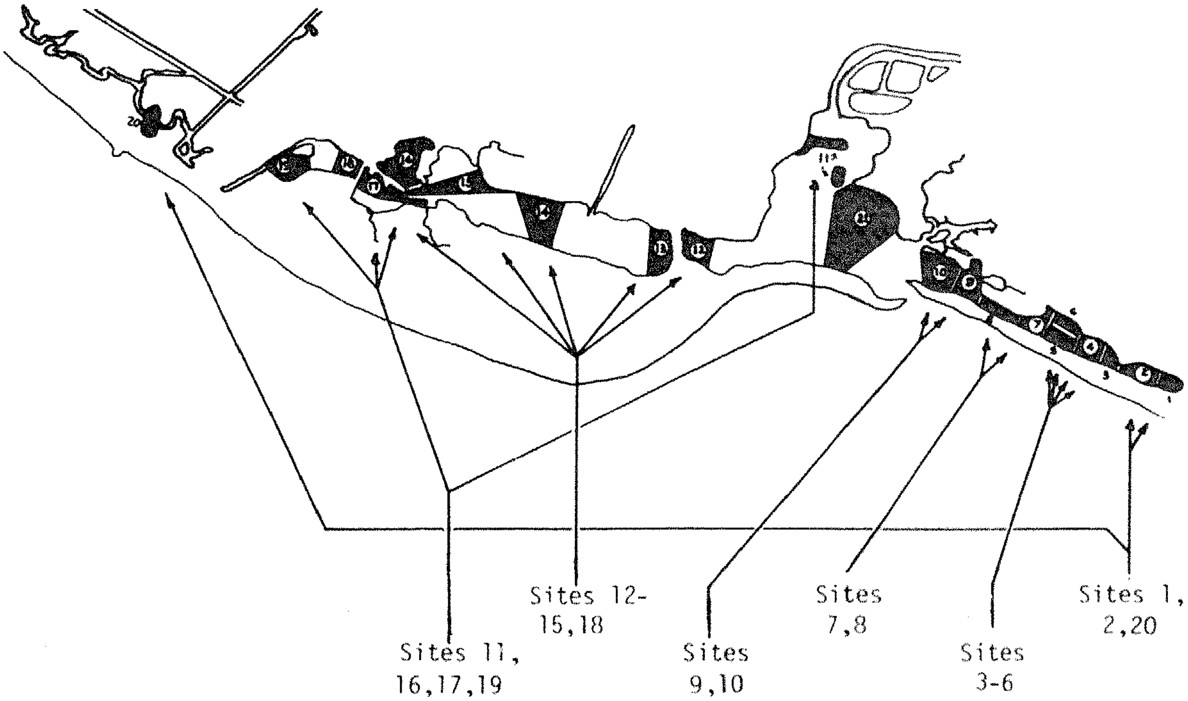


Figure 38. Five-year average abundances of water-related birds by month at census sites 1 through 20, Mugu Lagoon (Figure 39), arranged according to month of peak abundance from earliest at top left, to latest at bottom right.



Group #:	1	2	3	4	5	6
Coots	18.2	10.1	0.1	0.2	0.8	2.7
Surface-feeding shorebirds	29.2	10.9	1.3	3.8	1.9	5.3
Dabbling ducks and geese	4.3	1.2		1.9	2.5	0.8
Probing shorebirds	6.0	3.8	5.0	10.8	2.4	4.1
Wading fishers	0.2	0.1	0.1	0.2	0.2	0.2
Diving ducks	5.5	13.9	0.2	0.4	3.9	0.6
Diving fishers	0.5	1.3	0.1	0.3	0.9	0.2
Aerial fishers	1.6	0.5	1.3	0.6	0.2	0.1
Gulls	2.2	0.9	6.4	1.8	0.6	0.1
Others	0.1					
Total birds/ha	67.8	42.7	14.5	20.0	13.4	14.1

Figure 39. Bird census sites grouped according to >60% similarity in their densities of the indicated categories of water-related birds and the mean densities (no./ha) of each category in the different groups of sites.

According to these site associations, the salient features of habitats are as follows for the different categories of birds. Coots and surface-feeding shorebirds tend to correspond in their selection of habitats and favor sites with large expanses of mudflats and shallow open water. Presumably, the coots are somewhat more closely tied to the water in the mudflat-open water habitat and feed primarily on the sometimes thick mats of Enteromorpha; the surface-feeding shorebirds are more strictly confined to the tidally exposed portions and feed exclusively on small invertebrates on and just below the surface of the mud. The low densities of invertebrates that we documented for the extreme eastern end of the lagoon may explain the relatively low density of surface-feeding shorebirds in Group 1; however, this is speculation only since a 1-mm screen is too coarse to sample the prey of the birds satisfactorily.

The dabblers were most abundant at sites containing islands covered by marsh vegetation. Their distribution deviates strongly from that of the coots, which also dabble most of the time.

The large, deep-probing shorebirds and the wading fishers (egrets and herons) were similar in their relatively even distribution throughout the lagoon (Figure 39). Both categories are birds of the waterline. Apparently, whether a shore is steep or flat is of little consequence to these birds since they spend most of their foraging time close to the water's edge. The probing shorebirds are therefore distinct from the surface-feeding shorebirds in terms of a more linear vs. more areal dispersion. In addition, they are preeminently the birds of sand flats and sandy shores. While most other feeding types are rare here, the probing shorebirds are at their most abundant, as are large, deep-living infauna, their preferred prey.

The largest expanses of open water attracted the greatest numbers of diving ducks and diving fishers (Figure 39). The diving ducks feed mostly on invertebrates on the bottom. Ducks such as mergansers that dive for fish in the water column or on the bottom are classified with the other diving fishers (the grebes, loons, and cormorants). Gulls and the aerial fishers (mostly pelicans) were most common roosting on sandy islands near the tidal inlet. These they shared with hauled-out harbor seals. The aerial divers, in this case mostly terns, also roosted on another small island in Site 17 and a sand bar in Site 7 (Figure 39). Although terns, pelicans, and gulls feed inside the lagoon, we do not know how much foraging is done elsewhere.

There is little indication of long-term change in the total number of birds utilizing Mugu Lagoon based on our 5 years of records, although numbers were somewhat higher in the last 2 years than in previous years (Figure 40). Within categories, much larger changes are evident. For example, in the lagoon as a whole the number of coots has declined every year since 1977-78 (59% in 5 years). In contrast, the surface-feeding shorebirds have increased in every year since 1977-78 (96% in 5 years). Changes for other categories have been much less or, in the case of dabblers and gulls, erratic enough that it is impossible to determine whether the low numbers of the fifth year are part trend or merely fluctuation. The major sections of the lagoon contributed differently to these overall changes in number. Surface-feeding shorebirds, for example, were half as abundant in the last 2 years as earlier in the eastern arm, increased twofold in the western arm, and increased fourfold in the central basin (Figure 40). Coots decreased by almost a factor of three in the western arm, but changed little elsewhere. The abundance of gulls has increased substantially in the eastern arm and fluctuated in the central basin.

Although few censuses were conducted before the major storm of February 1978, there is no doubt that the filling of most of the central basin at that time was responsible for the increase in surface-feeding shorebirds there. Since probers, diving and wading fishers, diving ducks, dabblers, and coots were less abundant in 1977-78 than in any of the succeeding 4 years, it is possible that a shallower central basin has provided more satisfactory habitat for them as well. However, this is a suggestion, based on the limited sampling of the very large Site 21 before

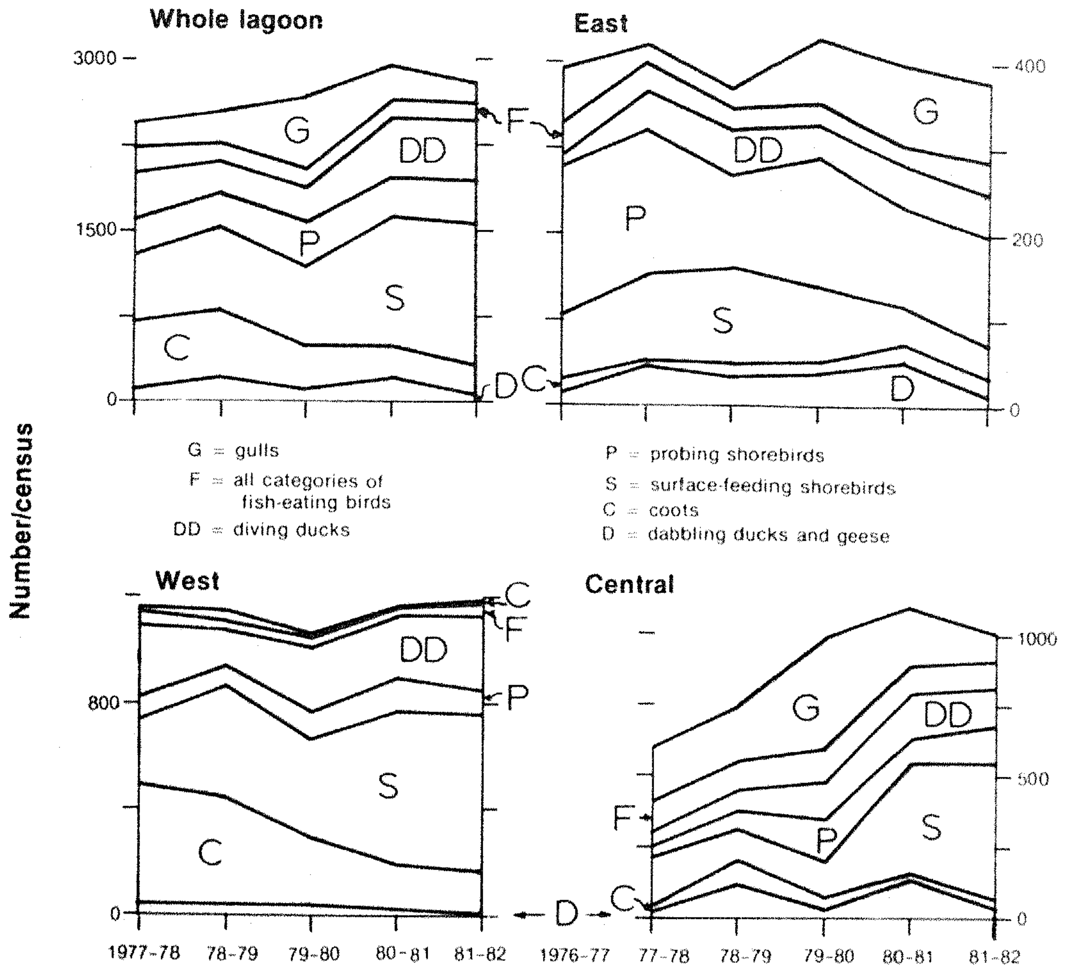


Figure 40. Changes in bird abundance over time at Mugu Lagoon.

June 1978, and not a conclusion. The partial shift in gulls probably had more to do with the extreme eastward migration of the tidal inlet in 1980 and 1981 than with the filling of much of the central basin, since gulls were most abundant on the shifting sand bars or islands associated with the inlet. In the western arm, the compensatory changes between coots and surface-feeding shorebirds are consistent with the possibility that sedimentation might favor the tidal flats element, i.e., surface-feeding shorebirds of the tidal flats-shallow open water couplet.

The additional year of censuses (1976-77) in the eastern arm before February 1978 allows more rigorous tests there for storm-related effects. Numbers of probing shorebirds were down in all 13 of the possible pair-wise comparisons between fall abundances before and after the storm of February 1978 (October - December 1976 and 1977 vs. 1978, 1979, 1980, 1981) and winter through summer abundances before and after (January - September 1977 vs. 1978, 1979, 1980, 1981, 1982). The diving fishers were down in 12 of 13 possible comparisons, whereas the diving ducks increased in all 13 comparisons. It is unlikely that these outcomes are chance events. The former two are consistent with the known decreases of large invertebrates and fish after the storm.

This analysis of Mugu Lagoon birds has been limited to common water-related species classified into functionally related categories or guilds: the birds that play important roles in the estuarine ecosystem. Other species are unimportant in the ecosystem because of their extreme rarity, but the ecosystem is critical for their survival, most notably the light-footed clapper rail (Rallus longirostris levipes), Belding's Savannah sparrow (Passerculus sandwichensis beldingi), and to a lesser extent the brown pelican (Pelecanus occidentalis) and the least tern (Sterna albifrons). These endangered species are more appropriately discussed in Chapter 7.

In addition to the water-related birds, at least 100 species of more terrestrial birds have been sighted around the lagoon (Macdonald 1976b; Natural Resources Management Office, U.S. Naval Air Station, Point Mugu, California; unpubl. list). Some commonly use aquatic habitats; for instance, swallows often are conspicuous either pursuing flying insects over water and marsh or gathering mud from creek banks for nests. Other species have an affect on the estuarine ecosystem. For example, large birds of prey could be important predators on the water-related birds. Nevertheless, the interactions between the more terrestrial birds and the estuarine ecosystem are assumed to be weak and have been ignored.

4.5 THE HERPETOFAUNA AND MAMMALS

Amphibians and reptiles appear to have even less of a role in the Mugu Lagoon estuarine ecosystem than the land birds. Eleven species have been reported (Natural Resources Management Office, U.S. Naval Air Station, Point Mugu, California; unpubl. list). Observations of western fence lizards (Sceloporus occidentalis) and side-blotched lizards (Uta stansburiana) are limited to adjacent uplands (Soil Conservation Service 1983). Southern Pacific rattlesnakes (Crotalus viridis helleri) have been encountered in the marsh, particularly after the flooding of 1978. Probably these animals were rafted into the lagoon on debris washed out of the watershed during the February 1978 storm.

Forty-one species of mammals are recorded for the Naval Air Station adjacent to Mugu Lagoon (Natural Resources Management Office, U.S. Naval Air Station, Point Mugu, California; unpubl. list). Of these, four species, the western harvest mouse (Rheithrodontomys megalotis limicola), California vole (Microtus californicus stephensi), ornate shrew (Sorex ornatus salicornicus), and black-tailed jack rabbit (Lepus californicus), are resident in the high marsh (Coulombe 1970). Hoof prints of mule deer (Odocoileus hemionus) have been seen along the sandspit shore of the lagoon (Onuf, pers. observ.), and a variety of terrestrial carnivores including the coyote (Canis latrans), red fox (Vulpes vulpes), gray fox (Urocyon cinereoargenteus), and striped skunk (Mephitis mephitis holzneri) frequently make forays into aquatic habitats. Probably the activities of the terrestrial mammals have minor effects on the Mugu Lagoon estuarine ecosystem. Coyotes and red fox den in the high marsh and beach ridge areas of the marsh. They are active resident predators and may have significant impacts on ground-nesting endangered birds.

The harbor seal (Phoca vitulina) is conspicuous within the lagoon proper. Over 100 seals can be seen hauled out on sand bars near the mouth of the lagoon. The number of harbor seals fluctuates with tides and time of year and averages around 40 (R. Dow, pers. comm.). This population is the only resident seal colony along the mainland shore of the Southern California Bight. Presumably, the isolation of the location from human disturbance is critical for residence by seals. Elsewhere along the mainland, shore sites may be used seasonally as rookeries or for hauling out, but not for year-round residence.

4.6 SUMMARY

The spatial and temporal patterns of the biota of Mugu Lagoon are anything but simple. The 10 to 20 species dominating each major division of the aquatic biota--plants, invertebrates, fishes, and birds--were distributed among several functional categories. Most taxa were found in at least a few physiographic units, but achieved maximal densities in a small subset of one unit. The exceptions were the marsh plants, which were confined to one physiographic unit, but were quite generally distributed therein. The microfloral films or mats, however, were present and important in all physiographic units.

Elevation appeared to be a minor determinant of distribution for most invertebrates (except that the salt marsh is distinct from the rest of the lagoon), since nearby intertidal and subtidal sites usually resembled each other closely both in kinds and densities present. Distance from the mouth of the lagoon had a greater effect on determining the distribution of different functional categories of invertebrates and was perhaps related to hydrodynamic characteristics. Only the California killifish exploited intertidal flats at high tide; the other fishes were more commonly associated with the subtidal areas. Conversely, the activities of the birds tended to concentrate in intertidal areas: the surface-feeding shorebirds feed on exposed flats almost obligately; gulls and most of the aerial divers roost on intertidal sand bars; the probing shorebirds and wading fishers feed near the tidally migrating waterline; and coots and dabblers feed in the very shallow water just beyond the tidally migrating waterline. Only the birds that dive for fish or invertebrates from the water surface and the aerial fishers (when feeding) concentrated their activities in deeper open water areas.

Only a few categories of organisms appeared to be sensitive to sediment texture and storm-caused changes in sediment texture. Probing shorebirds, large infaunal invertebrates, and eelgrass had obvious, strong affinities with predominantly sandy areas, while the opposite was true for surface-feeding shorebirds. New or previously rare taxa of small infaunal invertebrates became very abundant when true muds first appeared in the eastern arm; at the same time, the previously dominant taxa were eliminated. The blue-green component of the benthic microflora increased in response to the same change.

Although major changes in response to the storms were evident in many other taxa and categories, changes in elevation or depth generally seemed more important than textural changes. Examples include the large decline in the total catch of fishes in the eastern arm, most evident in species associated with deep areas; the shift in the distribution of salt marsh plant biomass; the increase in surface-feeding shorebirds (intertidal) and complementary decrease of coots (subtidal). Indirect changes also were important; for instance, the changes in shiner surfperch partly were in response to changes in eelgrass. The decline in the probing shorebirds in the eastern arm almost certainly resulted from the reductions in the densities of their large infaunal prey.

The final feature of note is the apparently intricate orchestration of the comings and goings of migrating birds and fish. Mugu Lagoon is dominated by birds in the cold half of the year and fish in the warm half. Dominant fish species or categories of birds with similar feeding habits vary month by month. It is not known whether this time-sharing is only a secondary consequence of some more important aspect of life history or whether it is a consequence of selection for exploiting a limited resource by a wide spectrum of short-term users.

The range of environments in Mugu Lagoon is such that only a few species or categories out of the small total pool are abundant in any one habitat, but those few are different between habitats and perhaps between times. Even though species overlap broadly, they must overlap in different portions of their respective tolerance or resource spectra to account for the large variety of distinguishable assemblages of organisms, each composed of such a small number of species.

Most of this description of the distribution and abundance of the biota of Mugu Lagoon is based on data collected in the eastern arm. The description of inner lagoon organism-habitat relations probably applies to large areas of the western arm and central basin. Except for the portion of the tidal delta in the central basin, there are no counterparts elsewhere in the lagoon of the sandy environments that are so prominent a part of the eastern arm. The consequences for birds have been described. Fish do not appear to be strongly influenced by this habitat parameter; however, many of the large invertebrates, especially the bivalves, are intimately associated with the sandy-bottom, subtidal channel. Consequently, large invertebrates probably are much less important in the rest of the lagoon than in the eastern arm. There is no persistent fresh or brackish water in the eastern arm. Consequently, possibly extensive areas along the Calleguas Creek channel in the central basin and at the western extremity of the western arm may not be represented in this profile.

CHAPTER 5. THE BIOTA: DYNAMICS AND INTERACTIONS

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Many relations of organisms with their physical environment inevitably were considered in Chapter 4 in the discussion of distributions. While some of those relations will be developed in more detail here, the emphasis will be on how groups of organisms interact. The discussion will generally follow the trophic structure of the lagoon.

The abundance and rate of change of abundance of any unit in the food web respond to factors at three levels: (1) food availability, (2) intra- and interspecific competition, and (3) predation. Of course, all these relations are modified by extrinsic variables such as temperature, substrate, habitat availability, and storms. Although identification of the linkages among the important organisms of any particular habitat is relatively easy, the determination of importance of the linkages, and measurement of the rates of change associated with those linkages are considerably more difficult.

Various researchers have taken three approaches to distinguish the effects of individual linkages or other factors on the dynamics of the Mugu Lagoon estuarine ecosystem. One might be called the blanket approach: measurement of a wide array of factors that could conceivably influence the rate at which a key process proceeds (the independent and dependent variables, respectively). Statistical procedures are applied to determine how much each independent variable "explains" the variation in the dependent variable. The second method is opportunistic and more direct. It capitalizes on extrinsically caused major alterations, such as by the storms of 1978 and 1980, that affect one or a few factors but not others, or some areas but not others. This isolates the effects of one factor or at least narrows the consideration to a few. The third approach is direct and planned. Manipulations are specifically designed to alter only one factor while not affecting others or to alter two or even three factors factorially. The latter allows not only the direct assessment of the effects of the different factors, but also determines whether they interact in any way.

5.1 PRIMARY PRODUCTIVITY

Shaffer and Onuf (1985) and Onuf et al. (1979) compiled preliminary estimates for the annual productivity of the different categories of plants in Mugu Lagoon (Table 8). The primary productivity of phytoplankton, benthic microflora, and submerged macrophytes was determined by dissolved oxygen techniques (Shaffer 1982). In simultaneous incubations of water samples and sediments submerged with filtered seawater at the same location, the benthic microflora were more than twice as productive as the phytoplankton in the water column over a similar area of bottom. Submerged macrophytes were ten times as productive as benthic microflora.

The distributions and life histories of the salt marsh vascular plants at Mugu Lagoon were such that net changes over a growing season simply could not express

Table 8. Primary productivity in Mugu Lagoon: estimates of annual productivity for different sources, the conditions to which the estimates apply, and conversions to similar units. GPP = gross primary productivity, NPP = net primary productivity, NAPP = net aerial primary productivity.

Source	Estimate of primary productivity as measured	Applies to	Factor to convert to g C m^{-2} y^{-1} NPP	NPP (g C $m^{-2}y^{-1}$) under conditions measured
Phyto-plankton	∿70 g C m^{-2} y^{-1} GPP[a]	Subtidal areas	NPP = 0.77 GPP[a]	50
Benthic microflora	170 g C m^{-2} y^{-1} GPP[a]	Intertidal flats when flooded + subtidal areas	NPP = 0.77 GPP[a]	130
Submerged macrophytes	∿1,700 g C m^{-2} y^{-1} GPP[a]	∿10% of intertidal flats when flooded + ∿10% of subtidal areas	NPP = 0.77 GPP[a]	1,300
Salt marsh macrophytes	290 g dry wt m^{-2} y^{-1} NAPP[b]	Low marsh	g C = 0.25 g dry wt[c]	70
	730 g dry wt m^{-2} y^{-1} NAPP[b]	High marsh	g C = 0.25 g dry wt[c]	180

[a] Shaffer (1982).
[b] Onuf et al. (1979).
[c] Winfield (1980).

much of the production. Therefore, monthly measurements were made on 50 - 300 tagged shoots of each of four species as the most direct measure of growth, turnover, and production (Onuf et al. 1979; Onuf, unpubl. MS). To give an idea how important the turnover component of production is, more shoots of *Salicornia virginica* died during the period of increase in the green parts of plants from January to August than the maximum number of shoots that were alive at any one time (Figure 41). Over the whole year this translated into a production of 2.3 times as much biomass as could be identified by net increase. The result was similar for the three other species to which the method applied. Production estimated from tagging was 3.7, 1.8, and 2.9 times the net change over the growing season for *Jaumea carnosa*, *Limonium californicum*, and *Batis maritima*, respectively (Onuf et al. 1979).

Only the most general comparisons are warranted among the productivity estimates for the different kinds of plants (Table 8) because of the difficulties involved in converting the various estimates into the

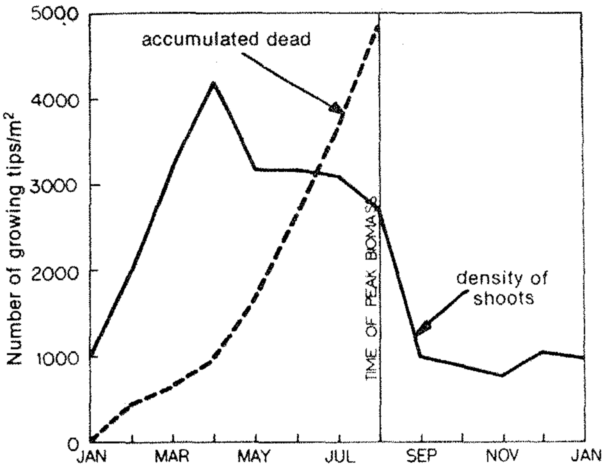


Figure 41. Density of shoots of Salicornia virginica in the lower marsh of Mugu Lagoon alive at different times during the growing season and accumulated dead since January.

same units and applying estimates to conditions other than those under which the measurements were made. For instance, the measurements of submerged macrophytes and benthic microfloral productivity were made under submerged conditions, yet both groups of plants occur intertidally as well as subtidally and are exposed to the air at least some of the time. Productivity probably is different in air than in water, especially at higher elevations where the sediment surface can dry completely, but we don't know how different.

Using high marsh sediment collected at Mugu Lagoon, Holmes and Mahall (1982) measured gaseous CO_2 exchange from initially flooded sediments as the sediments dried in an airstream. Photosynthetic rates of the benthic microflora increased, coinciding with the disappearance of a visible water film on the sediment surface, and remained higher than the submerged rate for 1 and 4 hours in two trials. Respiration exceeded photosynthesis after 3 and 6 hours of desiccation, at which times the water contents of the sediments were 85% and 75% of saturation, respectively. These results qualitatively suggest that exposed and submerged productivity may not differ greatly low in the intertidal zone (the sand and mud flats) where daytime exposure seldom exceeds 6 hours. High in the intertidal zone (the upper parts of the salt marsh), where exposure can last for days, productivity of exposed microalgae is bound to be much smaller than productivity of submerged microalgae.

The main caveat about the productivity estimates for the salt marsh vascular plants is the uncertainty arising from measurement techniques and calculations. The monthly estimates are imprecise because of the high spatial heterogeneity of the marsh. These errors are propagated in the mathematical manipulations used to generate the annual estimates.

Bearing in mind these essential qualifications about comparisons between kinds of plants, extrapolations to conditions not sampled, and shortcomings inherent in the techniques themselves, the contributions of various sources to the annual production of the eastern arm of Mugu Lagoon are indicated in Figure 42. Although the submerged macrophytes (mainly the green algae Enteromorpha and Ulva) are the most productive plants where present (Table 8), they cover a relatively small area in the lagoon on average over the year and make a relatively small contribution to the primary production of the entire system. The emergent vascular plants of the salt marsh and the benthic microflora of the flats and subtidal areas are, in comparison, only moderately productive; but by virtue of the large areas that they occupy, they heavily dominate total production.

Shaffer and Onuf (1983) sought to explain variation in benthic microfloral productivity by relating every determination of productivity to corresponding measurements of chlorophyll a, solar radiation, water temperature, community respiration, sediment composition, and initial dissolved oxygen for each sample. The multiple regression performed on the entire data set accounted for only 38% of the observed variation. When the multiple regression analysis was redone month by month and for sites grouped according to similar substrate history (similar responses to the major storm that occurred half way through the study; see

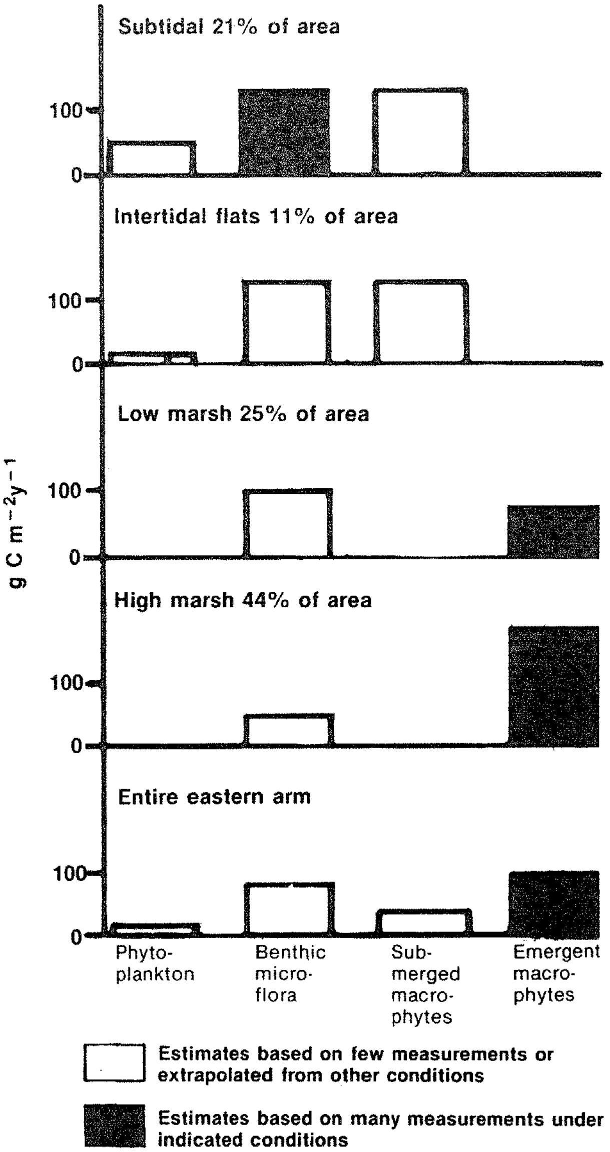


Figure 42. Contributions of different sources to the total net primary productivity of the eastern arm of Mugu Lagoon.

Figures 15, 16), the variance explained was much higher (60% of the average) than for the whole data set. In the monthly categorization, each of the six independent variables was most important during at least 1 month. Thus, the intuitively important factors were more important than the pooled analysis indicated, but not in the same way at all locations or at all times.

5.2 THE AVAILABILITY OF PRIMARY PRODUCTION TO CONSUMERS

Most of the plant material produced in Mugu Lagoon is separated spatially and temporally from most of the potential consumers, since most production is in the salt marsh and most consumers occur subtidally or in the intertidal flats. The biomass of some of the sources is too tough for most primary consumers of the ecosystem, increasingly so from the macroalgae Enteromorpha and Ulva through the submerged vascular plants Zostera and Ruppia to the emergent vascular plants of the salt marsh, especially those with woody parts such as Salicornia virginica. The nutritional quality of some of the sources is low for most consumers. In many cases this is strongly correlated with toughness. The high proportions of structural carbohydrates (e.g., lignin, cellulose) that make for toughness in plants require that too much biomass must be processed to obtain other necessary materials for maintenance, growth, and reproduction. For many aquatic consumers, amino acids are in critically short supply in these sources of primary production (Russell-Hunter 1970). Also, animals may lack the necessary enzymes for digestion, or palatability may be low.

There is almost no direct consumption (eating of live or recently dead plants) of the vascular plants of the salt marsh. The exceptions are (1) rare infestations by an unidentified scale insect and an unidentified moth larva on Salicornia virginica (Onuf, unpubl. observ.), (2) feeding by Belding's Savannah sparrows on the succulent tips of Salicornia and Suaeda plants when insects are rare (Massey 1979), and (3) parasitization by dodder (Cuscuta salina), presumably as much an herbivore as the sap-sucking scale insect. Thus, the primary consumption of most of this material is only after its death along a detrital pathway. Although macroinvertebrates often play a major role in the breakdown of this material, there is little or no indication that they directly assimilate the organic material of the plant. Rather, they assimilate the organic matter of the microbial decomposers on the surfaces of the detritus (Adams and Angelovic 1970). Perhaps the strongest evidence that the activities of the microbial decomposers determine the nutritional value of detritus for detritivores comes from Tenore's (1980) growth experiments on the deposit-feeding polychaete Capitella capitata, provided diets of detritus of different ages and from different sources. Growth was much more strongly correlated with microbial respiration than age or source.

The consequence of this intermediate step in plant utilization by macroinvertebrates is a decreased efficiency of transfer of carbon or energy from primary producers to the upper levels of the lagoon's trophic web. It also increases the time required to complete the transfer from primary producer to macrofauna. This increases the chance that something else might happen to that organic material produced within the system before utilization occurs within the system. The most likely alternative fates are export from the estuarine ecosystem to coastal waters by ebb tides or export in the opposite direction to the upland transition zone by spring high tides, especially when accompanied by strong winds, surf, or storm flows that can raise the stand of the water in the lagoon far above the normal tidal extreme. In this case, the productivity of the marsh is utilized mostly by terrestrial consumers. The physical separation of the potential subtidal estuarine consumers from the salt marsh source increases the likelihood that one of these alternative paths may be followed, especially when it is considered that most of the consumers are in or on the bottom, while much of the material in transit may be floating on the water surface.

The characteristics of phytoplankton and the benthic microflora that define their trophic relations are almost diametrically opposed to those just described for the vascular plants of the salt marsh (Table 9). These microbial plants are intimately associated with numerous consumers and are readily ingested and presumably assimilated. However, they probably leak their contents faster in life and after death than the salt marsh macrophytes, and this decreases their availability to macroconsumers. Also, they decrease in nutritional quality very rapidly after death, while the salt marsh macrophytes slowly increase. Despite these restrictions, the net result is that the trophic efficiency (proportion of the biomass of the plant converted into macrofaunal biomass) within the estuarine ecosystem is much higher for phytoplankton and benthic microflora, and much less is exported to some other system than for salt marsh macrophytes.

The differences in the availability of benthic microflora and phytoplankton to consumers are a consequence of mode of presentation (adhering to a surface vs. suspended in water). These differences probably affect the kind of consumer (deposit feeder vs. suspension feeder) more than the amount that is available for consumption, although the gelatinous sheath on some filamentous colonial epiphytic forms of benthic microflora might be an obstacle to herbivores as it can be in many freshwater systems (Porter 1977). Also, the difference in surface to volume ratios between planktonic and benthic occurrence should affect leaching rates. Finally, when benthic mats lift off the bottom en masse and float on the surface of the water, buoyed up by oxygen bubbles during periods of active photosynthesis (see Chapter 4), they are more likely to be stranded in the high-tide wrack than material suspended in the water column. Nevertheless, phytoplankton and the benthic microflora are trophically very similar in this system.

The submerged macrophytes are intermediate in their trophic characteristics between the extremes posed by salt marsh vascular plants and the microflora. Submerged macrophytes and the bulk of the macrofaunal primary consumers of the estuarine ecosystem are in close proximity. The submerged macrophytes are not immediately accessible to the infauna, but are only centimeters away and actually serve as the substrate for some surface-dwelling forms. They may be out of reach or too refractory for some or most consumers when alive but rapidly become more available after death (at least judging by their rapid rates of loss compared to marsh plants [Figure 43]). As a result of these characteristics, submerged macrophytes are likely to be used with moderate trophic efficiency within the estuarine ecosystem, and moderate quantities will be

Table 9. Factors reducing the utilization of a source of primary production by macroconsumers within the Mugu Lagoon estuarine ecosystem.

Factor	Phytoplankton	Benthic microflora (including epiphytes)	Submerged macrophytes	Salt marsh macrophytes
Physical or temporal separation between source & consumer	None	None	Small	Large
Live tissue unmanageable mechanically	No	Slightly	Moderately	Very
Live tissue low in nutritional quality	No	No	Moderately	Very
Aging required before consumption as detritus	No	No	Brief	Long
Export to coastal waters	Moderate	Moderate	High	High
Export to upland edge	No	Slight	Slight	Moderate
Leaching of dissolved organic matter from living plants	High	Moderate	Moderate to low	Low
Leaching of dissolved organic matter from dead plant material	Very high	Very high	Moderate	Moderate

exported to adjacent terrestrial and marine systems.

There is one possible qualification in this analysis of the trophic status of the submerged macrophytes. The very high levels of production that are possible locally and rapid decomposition can be too much of a good thing. The mats of decomposing seagrass or macrolagae can become so thick that the lower layers go completely anaerobic, turning the surface layers of the sediment into a black, hydrogen-sulfide-producing flocculent layer. Although some benthic invertebrates crawl into the overlying algae, the more sedentary organisms are probably killed (Onuf and Shaffer, pers. observ.). Clearly this will decrease trophic efficiency.

In summary, the characteristics and distribution of the phytoplankton and benthic microflora make them immediately available to a wide variety of macroconsumers. Most consumption of these plants probably occurs while they are still alive. Relatively little of the organic matter produced is exported beyond the production site. Therefore, phytoplankton and benthic microflora are probably used with high trophic efficiency within the estuarine ecosystem.

Submerged macrophytes are immediately available to some consumers but local productivity can be too great to be entirely consumed. Some, perhaps most, submerged macrophytes are consumed as detritus, soon after death. Some

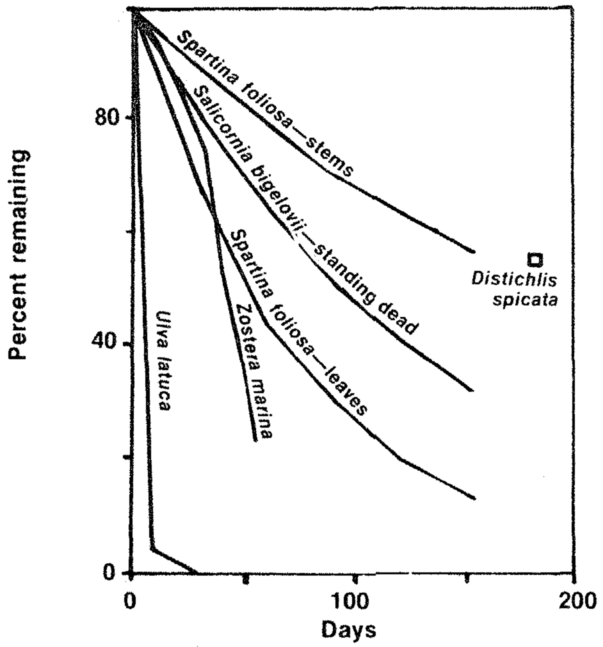


Figure 43. Decomposition in water of macrophytes that occur in southern California coastal wetlands (adapted from Nixon 1982 with values for Spartina foliosa and Salicornia bigelovii from Winfield 1980).

submerged macrophyte biomass is exported out of the estuarine ecosystem.

The salt marsh macrophytes are unavailable to most consumers until considerable aging as detritus has occurred. Much of their biomass probably is exported to coastal waters and to the terrestrial edge of the estuary. Consequently, salt marsh macrophyte biomass is used with low trophic efficiency within the estuary.

The preceding is a conceptual analysis, supported only by qualitative observations in Mugu Lagoon. Nevertheless, differences in the availability of the major primary producers to macrofaunal consumers will have major consequences for the trophodynamics of the Mugu Lagoon estuarine ecosystem. No quantitative estimate of the effect of differential plant availability on trophodynamics is possible; however, the differences in availability seem so large that primary production by itself is a poor indicator of the importance of a plant type in support of the lagoonal fauna. Considering the relatively high availability of benthic microflora and very low availability of salt marsh vascular plants, it is likely that the benthic microflora is the most important food for primary consumers in the lagoon, followed by submerged macrophytes, salt marsh vascular plants, and phytoplankton. In contrast, salt marsh vascular plants contributed most of the total estuarine primary production, followed by benthic microflora, submerged macrophytes, and phytoplankton (Figure 42).

5.3 PRIMARY CONSUMPTION

Typically, a food web is composed of several distinct groups of organisms at any trophic level. A major determinant of the structure of the next higher level is the separation among consumer groups according to which of the available food resources they exploit. The primary consumers of the Mugu Lagoon estuarine ecosystem are differentiated according to food source only to a limited extent. For instance, in the salt marsh, the snail Melampus olivaceus usually is associated with dense accumulations of Limonium californicum leaf litter, and judging by the feeding preferences of its similarly located congener M. bidentatus in Atlantic coast salt marshes, it feeds on that litter (Rietsma et al. 1982). On the other hand, Cerithidea californica, the other common snail in the marsh, grazes the sediment surfaces and the stems of the marsh plants. Although it also consumes fragments of the marsh plants, benthic microflora is its main nutritional source (Whitlach and Obrebski 1980). Finally, the crab Pachygrapsus crassipes scrapes the sediment surface when it feeds in the marsh (Onuf and Quammen, pers. observ.). Certainly it ingests the benthic microflora on the surface, but the detritus and organisms in the sediment immediately below the surface are likely to be much more heavily exploited than by Cerithidea.

In other parts of the ecosystem, niche separation according to source of primary production is less evident. The only obligate grazers on the submerged macrophytes are the California brown sea hare (Aplysia californica) and brant, and they are found only occasionally within the lagoon. Coots and dabbling ducks feed upon submerged macrophytes, but also take small invertebrates in the sediment. The crab Hemigrapsus oregonensis certainly is capable of shredding live macrophytes and will grow well in the laboratory provided solely with Enteromorpha (Kuris and Mager 1975); however, in nature it feeds on diatoms as well (Morris et al. 1980) and is a scavenger and a predator (Chapman et al. 1982). As for the rest of the primary consumers, they depend mostly on the same food: small organic particles, probably with little discrimination as to origin, whether they are true phytoplankton, benthic microflora, fragments of submerged macrophytes, or detritus derived form salt marsh vascular plants. Also, a wide variety of organisms are, to a limited extent, capable of uptake of dissolved organic carbon (Stephens 1982). Bacteria and other microbial decomposers are important nutritional sources and are consumed mainly in association with detrital particles.

Apparently, locational factors and the physical characteristics of habitats are much more important than plant type in explaining the relatively great variety of primary consumers in the Mugu Lagoon estuarine ecosystem. Thus, very different organisms will use the same fine-particled organic material, and they will do so in very different ways depending on whether: (1) it is suspended in the water column, adhering to surfaces, or mixed in sediments; (2) the sediment is sandy or muddy; (3) the location is never exposed to air or seldom flooded; (4) water movements are fast or slow; or other factors.

The bivalve mollusks and ghost shrimp provide the best illustration of how the primary consumers of Mugu Lagoon are partitioned in the apparent absence of different food sources. Peterson (1977), following Warme's (1971) analysis, described three distinct assemblages in the eastern arm according to the substrate type with which they were associated. The sand community (95%-98% sand, i.e., particles ≤ 0.06 mm) occurred in the subtidal channel, which connects the subtidal ponds of the eastern arm to the mouth of the lagoon (Figure 13). The "mud" community (actually 50%-90% sand) occurred in the western subtidal pond, and the muddy-sand community occupied a narrow transitional zone between the other two communities, extending especially along the south shore of the subtidal pond beyond the entry of the subtidal channel (Figure 13).

The three communities were characterized by very high volumes of macroinvertebrates, dominance by five or six species, dominance of suspension-feeding, and strong stratification among species according to their depth in the sediments (Figure 44). Ordinarily, several species exploiting the environment in the same way would not be expected to coexist in the same place (Gause's competitive exclusion principle). There are three general explanations for how similar organisms can coexist. Their densities can be held below the level at which competitive exclusions occur by: (1) physical disturbance (temporary extreme conditions that cause mortality), or (2) losses to natural enemies (predators, parasites, or pathogens), or (3) resource partitioning (niche differentiation).

The very high volumes of organisms (6,000 to 8,200 cm^3 of organisms/m^2 of bottom) that are continually present suggest that populations are at or near carrying capacity, thus eliminating explanations (1) and (2). However, tests so far have failed to demonstrate the necessary selective feeding among filter-feeding bivalves (Vahl 1973) to make partitioning of the food resource a possibility. These considerations, together with the clear evidence of depth stratification, led Peterson (1977) to infer that competition was the main factor responsible for the organization of all three communities, but that space, rather than food, was the resource in short supply. According to this interpretation, organisms should be much more sensitive to changes in the densities of organisms in the same depth than to changes in the densities of organisms in other strata.

Several independent lines of evidence bear on this hypothesis. The ghost shrimp, Callianassa californiensis, overlaps broadly in depth in the sand community with the clam Nuttallia (Sanguinolaria) nuttallii (Figure 44a); however, in individual samples, where one is abundant, the other tends to be rare. Thus, whereas

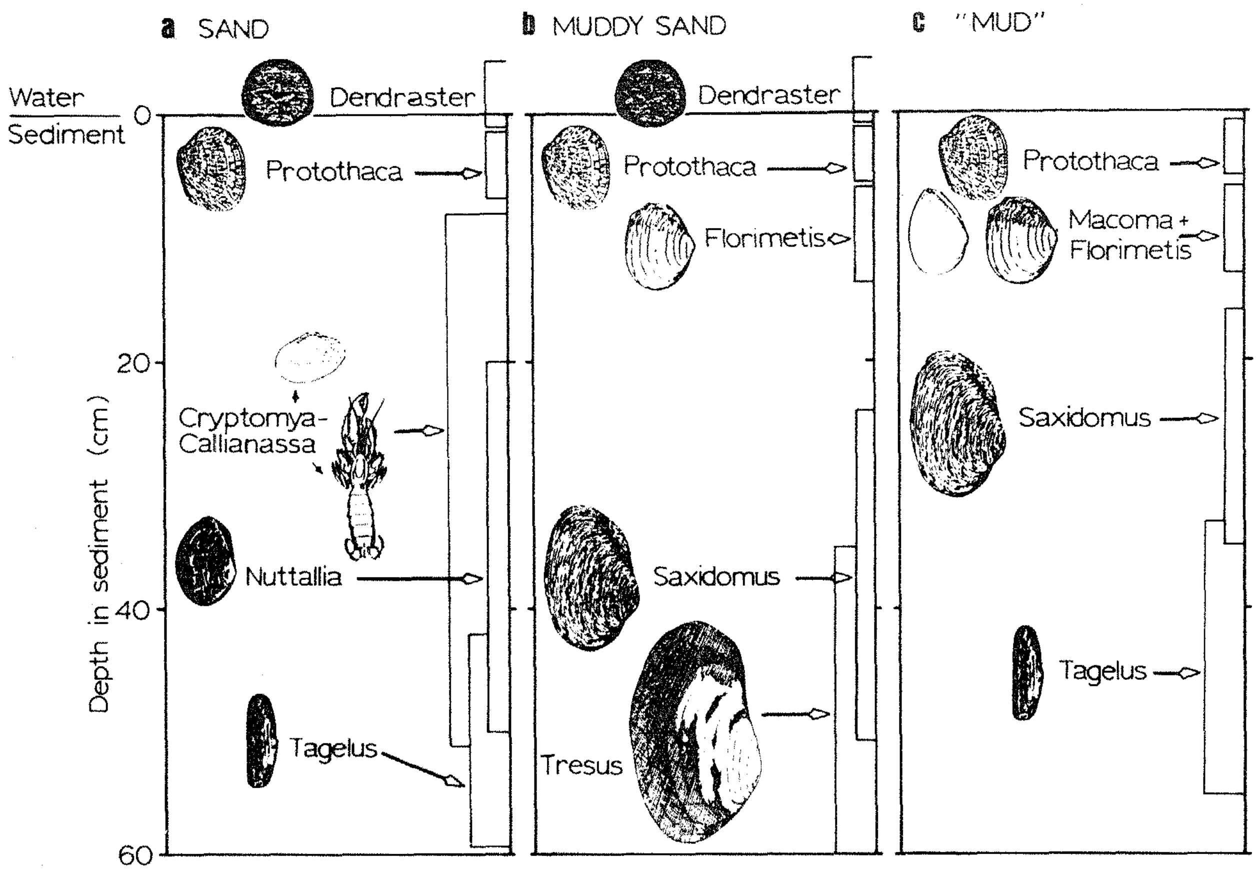


Figure 44. Stratification in the depth of living position of the abundant shelled invertebrates in sand, muddy-sand, and "mud" habitats of Mugu Lagoon, based on hand-dug samples (adapted from Peterson 1977).

niche overlap is broad in the horizontal plane for many inhabitants of the community and narrow in the vertical dimension, the opposite is true for Callianassa and Nuttallia. After Peterson (1977) eliminated all Callianassa from part of an area where they had been abundant, juvenile Nuttallia were 60 times more abundant than where Callianassa had not been removed. Apparently, Callianassa's intense reworking of the sediment (all the sand to a depth of 50 cm in a few months, according to MacGinitie's [1934] calculation) killed newly settled Nuttallia by burial or perhaps ingestion. Alternatively, Nuttallia larvae may have selectively settled in the removal area, responding to physicochemical changes in the sediments, such as increased anoxia.

The mechanism that seems to determine Nuttallia's abundance and size in the muddy-sand community is almost the exact antithesis of that just described for the sand community. Here, its depth range is occupied by two very large clams, Tresus nuttallii and Saxidomus nuttallii, three to four times as large as Nuttallia, with large siphons extending to the surface. When Nuttallia were introduced to the muddy-sand community in the presence of different species of the natural community and in isolation, their growth was unaffected by the surface dwellers (the clam Protothaca staminea and the sand dollar Dendraster excentricus). But growth was depressed ∿80% by the presence of the occupants of their preferred depth stratum (Tresus and Saxidomus) (Peterson and Andre

1980). Also, there was an increased tendency for Nuttallia to emigrate in the presence of Tresus and Saxidomus.

In an additional experimental treatment, in which live Tresus and Saxidomus were replaced by shells filled with sand and fitted out with surrogate siphons made out of wood, the growth of Nuttallia also was reduced significantly. In contrast, surface-dwelling Protothaca were not affected by the presence of either Nuttallia or Tresus and Saxidomus, even though all four species are suspension feeders presumably exploiting the same food. "Thus, while no apparent interactions occur between species which occupy different living positions in the sediments, species which share a similar depth stratum interact strongly, suggesting that competition for space is the primary mechanism of interaction in the system" (Peterson and Andre 1980).

Peterson (1982) provided yet another perspective on the role and type of resource competition in determining the structure of the Mugu Lagoon benthic community. Protothaca staminea and Chione undatella are the most common shallow-dwelling bivalves in the sand and mud communities described above. They are both classified as suspension feeders, are similar in size and shape, and are closely related taxonomically. Although it was reasonable to expect that these species would interact strongly, this was not found to be the case. Peterson's manipulations of densities of the two species alone and together demonstrated intense intraspecific competition, but interspecific interaction was weak or absent, even in the presence of the other species at eight times its normal density.

Competition for space could not be the major form of intraspecific interaction in these experiments, because, even at the highest densities of both species in the same enclosures, only 11% of the available area could possibly be occupied (assuming all individuals were at precisely the same depth). Therefore, intraspecific food limitation must be the cause of the observed competitive interactions. The required feeding separation between species that are so similar in morphology, distribution, and function is achieved by the positions of their siphons in feeding. The siphons of actively pumping Chione are always visible at the sediment surface and those of Protothaca never protrude, even though excavations reveal that a high proportion of their siphons are extended beneath the surface. Coincidentally, the frustules of benthic diatoms are abundant in the guts of Protothaca but have not been seen in the guts of Chione (Peterson 1982).

The upshot of these experiments is that position and location within sediments appear to be much more important than food source in accounting for the variety of primary consumers in the Mugu Lagoon estuarine ecosystem, at least as exemplified by the shelled macroinvertebrates.

Two major trophic groups, the suspension feeders and the deposit feeders, have been distinguished in the benthic macroinvertebrate community (Peterson 1977), but this distinction is far from straightforward. For example, two deposit feeders were volumetrically important in the communities studied by Peterson: the clam Macoma nasuta (22% of the volume of organisms present in the mud community) and the ghost shrimp (Callianassa californiensis) (20% of the volume of organisms in the sand community). Even though Macoma resides about 10 cm below the surface, it extends its siphon beyond the surface and sucks in the organic-rich layer at the sediment-water interface, according to most accounts (Morris et al. 1980; MacGinitie 1935). Alternatively, Ronan (1975) and Reid and Reid (1969) asserted that M. nasuta is primarily a suspension feeder.

According to a classic description by MacGinitie (1934), Callianassa feeds on subsurface organic material in the course of its prodigious burrowing activities. However, Devine (1966) reported that surface diatoms were the most conspicuous item in the guts of a New Zealand congener year-round, suggesting exploitation of surface material. At Bodega Bay, California, Ronan (1975) implicated surface material as an important part of Callianassa's diet, while Powell (1974) ascribed a filter-feeding habit on the basis of the morphology of the foregut and the scarcity of organic material in the sand where they occurred. Judging from the low sediment carbon values in Warme's (1966, 1971) analyses for the sand channel, filter feeding may be necessary at Mugu Lagoon as well.

The biology of other primary consumers in Mugu Lagoon is not well studied. The four small crustaceans that have been abundant at least sporadically in the eastern arm between 1977 and 1982 are associated with compacted sediments and hard surfaces (the gammaridean amphipod Corophium acherusicum), the surfaces of macrophytes (another gammaridean amphipod, Pontogeneia opata), and unconsolidated fine sediments (the caprellid amphipod Mayerella acanthopoda and the cumacean Oxyurostylis pacifica). They either scrape surfaces, process loose particles on a surface or suspension feed (J.W. Chapman, EPA, Newport, Oregon; pers. comm.). Only Pontogeneia is likely to exploit other food sources in addition to the small particle mix of benthic microflora and detritus. Encrusting animals as well as macroalgae are prominent inhabitants on the surfaces of macrophytes and may be eaten by Pontogeneia. Thus, locational factors appear to be more important than diet in niche differentiation for the small crustaceans as well as for the bivalves and ghost shrimp.

No one has studied the feeding habits of the soft-bodied invertebrates at Mugu Lagoon in detail; however, generalizations may be made based on studies elsewhere on the same or related species.

There are three modes of primary consumption among the soft-bodied invertebrates of Mugu Lagoon: suspension feeding, surface-deposit feeding, and subsurface-deposit feeding while burrowing. All are based on fine particulate organic matter. As with the clams and Callianassa, the distinctions among feeding modes are blurred. For instance, in a study of feeding in three species of spionid worms normally classified as surface-deposit feeders, Taghon et al. (1980) demonstrated changes between deposit feeding and suspension feeding, depending on the flux of particles passing by in the water column. Alternatively, Jumars et al. (1982) reported an abrupt switch to "a decidedly macrophagous, predatory mode" when small crustaceans swam into the tentacles of two of these species. These findings almost certainly are of significance in Mugu Lagoon. Half of the "small worm-like" taxa listed in Table 4 are spionids. Furthermore, the animals used in the studies cited above, collected on San Juan Island, Washington, were in the same shallow-water, soft-bottom environment as in Mugu Lagoon.

As with the other major groups of primary consumers, spatial separation of soft-bodied invertebrates is conspicuous. Depth stratification is implicit in the names of trophic groups that exhibit suspension feeding, surface-deposit feeding, or subsurface-deposit feeding (above, on, and under the sediment surface). In addition, Whitlach (1980) documented vertical stratification within the sediments in his study of the deposit feeding communities of Barnstable Harbor, Massachusetts, as well as horizontal differentiation. In particular, he observed that many more species co-occurred in samples rich in organic matter than in samples that were poor in organic matter. Furthermore, those that were abundant across the whole range of sediments sampled overlapped less with other species in depth distribution and particle size utilization than those that occurred only where organic matter was abundant. Whitlach (1980) inferred from these patterns that competitive interactions were important determinants of the organization of the deposit-feeding guild. When food was meager, only those few species that were distinctly different in their feeding characteristics, especially feeding location, could co-occur. When the organic content of the sediments was high and presumably food was abundant, these species were joined by others that overlapped broadly with each other and with those already present in both their vertical distributions and particle-size utilizations. Density-dependent predation, interference among conspecifics at high densities, or some other factor may have to limit the specialists when food is abundant. Otherwise, why don't the specialists increase to the point that food again is too meager for generalists, regardless of the rate of supply?

Despite uncertainties about the precise mechanism of interaction among the soft-bodied invertebrates, biological interactions are major determinants of the organization of this group. Spatial differentiation is one manifestation of those interactions. Although the analysis of factors involving the relations among the soft-bodied invertebrate primary consumers relies on information collected in other geographic regions, conclusions are similar to those from the detailed studies of the shelled invertebrates at Mugu Lagoon. Namely, a high level of spatial segregation allows a varied assemblage of consumers to subsist on essentially the same food resource.

5.4 PREDATION

In Mugu Lagoon, secondary consumers are confronted with a wider choice of possible foods than the primary consumers. Of course, the secondary consumers are confronted with the same challenges posed by the physical environment as are the primary consumers. Secondary consumers can exploit their food resource selectively by keying in on a specific prey (for instance, ambush predation by halibut on crustaceans or other fish) as well as by keying in on a specific physical environment (for example, shallow-feeding shorebirds feeding on a mudflat).

Birds and fish, the two most obvious categories of secondary consumers and probably the most important, are constrained first by characteristics of the physical environment. Shorebirds are limited to intertidal areas and can use them only when they are exposed at low tide. It is equally obvious that fish and diving ducks are limited to areas covered by water. Although this does not preclude their use of intertidal areas, it reduces the availability of those areas compared to areas that are always submerged. As described in the previous chapter, there was no discernible difference in the species composition or abundances of invertebrates between intertidal and subtidal benthic samples in the same general area of the lagoon. This suggests that, at least at the grossest level, differentiation of the physical environment is more important than differentiation of the food supply in determining the organization of the secondary-consumer trophic level. (This analysis may not apply to the small crustaceans, because they were not adequately sampled by the techniques used.)

The most conspicuous predatory activity in the Mugu Lagoon estuarine ecosystem is the scurrying about of shorebirds on the mudflats, sticking their bills into the mud every few seconds and presumably pulling out something to eat much of the time. Since small worm-like invertebrates are usually the abundant organisms near the surface of the mud, it is reasonable to infer that they are the principal prey of the shorebirds. Given the abundance of the shorebirds, it is likely that they consume many worms; however, that is as far as reasonable inferences can go. It cannot be said whether predation substantially reduces the densities of worms, alters the relative abundances of different species or, if either of these occurs, whether the shorebirds are responsible for the effect (rather than fish that can forage on the mudflats at high tide).

A number of field experiments at Mugu Lagoon and Upper Newport Bay, California, have elucidated the predator-prey relationships between shorebirds and soft-bodied benthic invertebrates (Quammen 1981, 1982, 1984). At a muddy (8% sand) site studied by Quammen, benthic invertebrates were much more abundant in summer than in winter (Figure 45a), when surface-feeding shorebirds were abundant (Figure 45b), and their feeding activity was intense. At a muddy-sand (80% sand) site, densities of the same invertebrate species were higher in summer than in winter (Figure 45a). The differences in seasonal abundance were explained by both predation and site characteristics. When shorebirds were experimentally excluded at the muddy site, infaunal densities remained high throughout the year, clearly pointing to predation as a major factor in controlling infaunal abundances. Quammen found, however, that the addition of a thin layer of sand to muddy sediments reduced shorebird feeding activities by more than half. The added sand did not alter the mud surface visually, nor the density of the worms in the top 2 cm of sediment, suggesting that coarse particles at densities higher than 8% in surface layers of mudflats deter

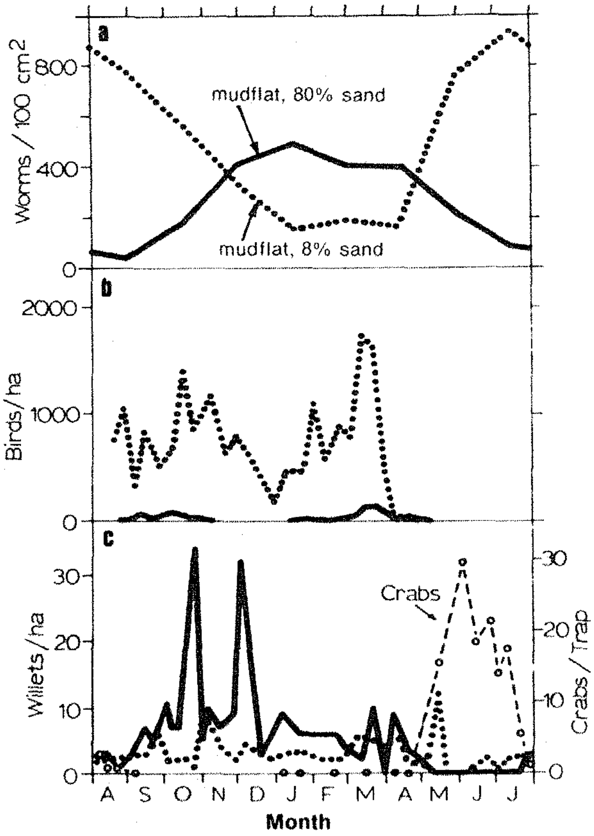


Figure 45. The abundances of worms, surface-feeding shorebirds, and crabs and willets through the course of a year at two locations varying in sand content of the substrate. Crabs were not present at the muddier site.

shorebird feeding, probably by interfering with prey capture.

Predation controlled the infaunal abundance at the muddy-sand site, but in a different manner. Use of the site by surface-feeding shorebirds was much lower than at the muddy site (Figure 45b), perhaps in part due to the interference of coarse-grained sediments described above. Another predator, the lined shore crab (Pachygrapsus crassipes) was abundant during the summer at the site (Figure 45c), but was absent at the muddy locations. When the crab was abundant, infaunal densities were low. When crabs were excluded, densities of the benthic invertebrates increased relative to those outside the exclosures. In the winter, when the crabs were not present, densities inside and outside the exclosures were similar. Thus, crabs, not shorebirds, were the major predators on the invertebrates in the muddy-sand sediments. However, even here, shorebirds (in this case, the large probing shorebirds rather than the small surface-feeding shorebirds) may be ultimately responsible for the seasonal pattern of abundance in infaunal invertebrates. Large shorebirds, especially willets, preyed heavily on the crabs when both were present on these flats for a brief overlapping period in the late summer (Figure 45c). Thus, the absence of crabs, perhaps in response to the relatively high densities of willets, together with the low abundance of surface-feeding shorebirds, accounted for the high winter populations of the soft-bodied invertebrates in "sandy" mudflats.

In summary, predation, especially by shorebirds, is a major influence on the small soft-bodied primary consumers inhabiting mudflats. The influence is a strong seasonal effect on abundance because of the migratory habit of shorebirds. Predation may produce opposite patterns of seasonal abundance on intertidal flats, depending on the amount of sand in the substrate and whether the shorebirds prey directly on the worms of the mudflats (surface-feeding shorebirds where little sand is present) or on the crabs that prey directly on the worms. Although not explicitly stated above, another important characteristic of these interactions is that there is no obvious effect on the relative abundances of prey taxa; i.e., apparently there is little selection among prey or differential response such as might be expected for prey with different life histories subjected to the same intensity of predation. Changes in the relative abundances of different taxa are more common in other systems. Physical factors seem to be much more important in defining the characteristics of the trophic interaction than what prey are eaten.

Peterson's (1982) exhaustive study of the population biology of the similar and related bivalves Protothaca staminea and Chione undatella provides a strong contrast to the preeminence of physical factors over characteristics of the prey in determining the features of the linkage between primary and secondary consumer levels. Here, despite similar position in the substrate, shape, and to a lesser extent size, *Protothaca* suffered relatively high mortality, mostly attributable to a variety of predators. In contrast, mortality in *Chione* generally was low, and little or no mortality was caused by predation. Apparently, *Chione*'s slightly bigger size and heavier shell at all sizes made it essentially immune to predation. In complement to these survivorship patterns, recruitment by *Protothaca* was over an order of magnitude higher and less variable from year to year than recruitment by *Chione*.

For the most part, fishes in Mugu Lagoon are not major consumers of infauna. A partial exception is siphon-nipping (partial in the sense that the victim survives, unlike the victim in most predator-prey interactions). For *Protothaca*, the effect of siphon-nipping can be considerable, depending on location.

Peterson and Quammen (1982) observed that the growth of *Protothaca* in the clean sand environment at Mugu Lagoon was over twice as great inside cages that excluded large predators (6-mm openings) as in cage controls or open areas, but that there was no difference in the muddy sand environment. This suggested that the presence of predators affected growth in one area but not the other. Observations of *Protothaca* in aquaria eliminated the possibility that reduced growth was the consequence of closing up for protection in the presence of potential predators. *Protothaca* fed just as actively in the presence of a variety of predators as in their absence. Clam siphons were common in the guts of two fishes, the staghorn sculpin (*Leptocottus armatus*) and the diamond turbot (*Hypsopsetta guttulata*). Reduced growth would be an expected cost of regenerating the siphon. Also, feeding efficiency is likely to be lower until the feeding organ is fully replaced. Therefore, the cropping of siphons by fishes probably accounts for the enhanced growth of *Protothaca* within exclosures in the clean sand environment.

The interesting thing is that there is no such reduction in growth in the muddy-sand environment, despite higher densities (2.3x) of the two important croppers and siphons occurring more frequently (1.8x) in their diets. The explanation is simple. Not only was *Protothaca* much denser in the muddy sand site than in the clean-sand site (2.7x), but also another bivalve, *Macoma nasuta*, was even denser than *Protothaca* (2.9x). The net result was that *Macoma* bore the brunt of the cropping (70%) in this environment as determined by identification of siphons in guts to species. The remainder was distributed over a bigger population of *Protothaca*, such that the cropping rate per individual was at least 40% lower than in the clean sand. Thus, in this case, the presence of an alternate prey accounts for a difference between locations in the outcome of a trophic interaction.

We know the other feeding activities of fishes from analyses of their gut contents (Table 10), but the effects on lower trophic levels have not been worked out in such detail as the cases described above. Some species concentrate on a narrow range of food. Large California halibut, for instance, feed mainly on other fishes, while large topsmelt contain (feed on?) plant material and mud (or the diatom film associated with it?), and large shiner surfperch eat mainly small crustaceans (gammarid and caprellid amphipods, and cumaceans). However, the diets of these latter two species change ontogenetically. The smaller sizes of both species eat zooplankton almost exclusively. The other species listed in Table 10 have more varied diets. For instance, small crustaceans and gastropods were most important for California killifish, whereas polychaetes, mollusk siphons and large crustaceans were most important for diamond turbot.

Despite the variety of foods consumed by the fishes of Mugu Lagoon, two common trends are evident. First, the feeding activities of the fish tend to be focused at sediment or submerged plant surfaces or in the water column rather than in the sediment. Only the sixth most abundant fish, the diamond turbot, commonly consumed buried prey (polychaetes), and even then other items were at least as important. In this characteristic, the fish are almost diametrically the opposite of

Table 10. The gut contents of fishes in Mugu Lagoon, February 1977-January 1978, all stations (see Figure 34) and months combined. See Table 4 for the taxonomic composition of most prey categories. O = overwhelming predominance, V = very important, I = important, C = common, P = present.

		Food types									
Species	Number examined	Small polychaetes (small worm-like)--in sediments	Small gastropods--on bottom	Mollusk siphons--in or at surface of the sediments	Microcrustaceans--on surfaces and in water column	Peracarids (small crustaceans) --on surface and in water column	Crabs and shrimp (large crustaceans)--on surfaces and in water column	Fish--on the bottom and in the water column	Plants	Mud	Empty
Topsmelt	170				C				I	V^a	
Shiner surfperch											
<100 mm	133				V	V^b					
>100 mm	51					V^c				O	I
Staghorn sculpin	153	P	P	I	P	I^d	I^e	I			
California killifish	86	P	I^f	C	C^g	I^b	P	C^h		P	C
California halibut											
<100 mm	31	P		C		I^c	V^i	I^k			
>100 mm	14			P			C	O^k			
Diamond turbot											
<100 mm	55	V		C	C	C^c	C	I^m			
>100 mm	36	I		I		C^c	I^e	I^m			
Bay pipefish	84					V^d	C^i	C^o			

[a] Diatom film?
[b] *Corophium*
[c] Cumacean
[d] *Pontogeneia*
[e] *Hemigrapsus*
[f] *Acteocina*
[g] Ostracod
[h] Fish eggs
[i] Grass shrimp
[k] Goby
[m] Fish embryos
[o] Fish fry, embryos, and pipefish.

the shorebirds, the other important secondary consumers of Mugu Lagoon, since the shorebirds consume polychaetes and other invertebrates living in the sediments to a greater extent than species that live on the surface or in the water column. Thus, the two groups of secondary consumers are complementary in what they feed on as well as where and when (seasonally and during a tidal cycle) they feed.

The other trend is the prevalence of crustaceans in the diets of the fishes. This is especially true of the small crustaceans, important at some stage of life to all fish species except the topsmelt. The converse does not appear to be true, however: important as small crustaceans may be to fish, fish do not appear to have much effect on the populations of small crustaceans. This is the tentative interpretation of the following observations.

Chapman et al. (1982) generated relative measures of the intensity of predation by fish on small crustaceans from analyses of the gut contents of all the common fishes of Mugu Lagoon combined with monthly determinations of fish abundances. There was no indication of responses by the prey population even under the particular conditions when an effect of the fish would seem most likely. Amphipod and cumacean populations did not decline when the rate of their consumption by fish was highest relative to the density of small crustaceans any more often than when the consumption rate was low relative to prey density.

Of course, the importance of predation can be expressed in another way. A behavior of a prey that can be demonstrated to reduce its losses to a predator is likely to be an evolutionary adaptation to predation. Predation still might be a major factor in the biology of an animal, even in the absence of losses to predators at present, if the present immunity has resulted from behavioral adaptations that reduced predation. Vertical migration (nocturnal forays from the bottom or from the surfaces of plants into the water column) by the small crustaceans of Mugu Lagoon (Figure 46) could be a case in point. Because the time spent in the water column is always during the night, investigators elsewhere have proposed that vertical migration could be adaptive for avoiding diurnal visual predators such as fish. Experiments conducted in Mugu Lagoon do not support this hypothesis. There is no clear evidence of a major role for predation in the biology of the small crustaceans in Mugu Lagoon.

5.5 HIGHER TROPHIC LEVELS

We have almost no information on the trophic interactions beyond the secondary consumers. Higher-level predators are primarily piscivorous birds and fish. Spatial segregation is obvious among the major groups of high-level predators. The wading fishers (Table 7), mainly herons and egrets, confine their activities almost exclusively to shallow water near the waterline. The aerial fishers, mainly pelicans and terns, prey on fish in the surface layers and visible from the air. The diving fishers, mainly grebes, may exploit bottom-dwelling fish in the deeper parts of the lagoon. The most important piscivorous fish is the California halibut (Paralichthys californicus) (Table 10), which spends most of its time on the bottom.

Observations about the feeding of the top level predators in Mugu Lagoon are difficult to obtain. In most cases the prey are consumed too fast to identify what is being eaten. We know that eared grebes eat diamond turbot because the birds have such a hard time eating them; however, we know nothing about the meals (if any) that went down easier. Also, gulls and terns obviously eat topsmelt because they stick so far out of the bills, but we know nothing about the birds' predation on other fishes.

One possible indication of an overall effect of top predators on populations of the most common species of fish is the numerical decline of fish in our catches in the few months after their peak abundances (Figure 35). Assuming that mortality is the major source of numerical change (an untested assumption) and that predation is the major cause of mortality in this period, fishes big enough to be caught with our seine decline ∿20% per month (Figure 47). With the exception of

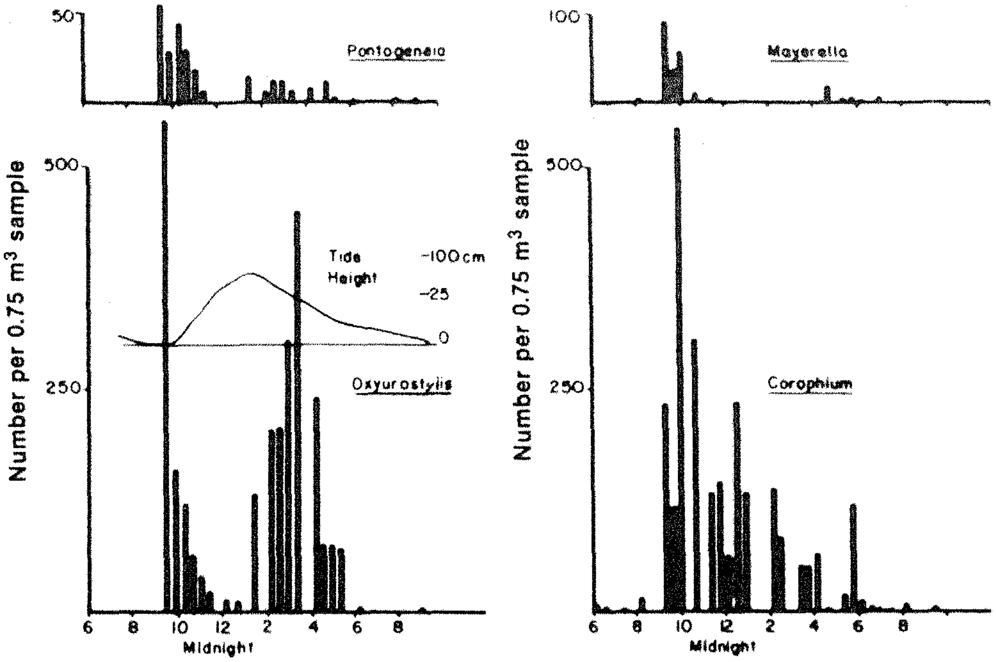


Figure 46. Plankton samples collected in the eastern arm of Mugu Lagoon at approximately hourly intervals on 7-8 August 1978. Tide height was measured from low water in the eastern arm. Reduced abundances between 10 p.m. and 2 a.m. correspond to increased tide current velocities (from Chapman et al. 1982).

staghorn sculpin, the rates of mortalities appear to be constant from month to month and similar between species.

The two major categories of predators - birds and fish - have a common high mobility throughout life and relatively long lives. These characteristics free the predators from controls that the estuarine environment would impose if they were constrained to be full-time residents. However, here the resemblance ceases. The lagoon is at opposite termini for bird and fish migrations. The Arctic imposes strict seasonality on the birds. It provides incredibly rich food for the rearing of young but prohibits the presence of birds in the winter. Although prey tend to be more abundant and almost certainly more productive during the summer in Mugu Lagoon, the even greater richness of the Arctic during this season is a sufficient inducement for birds to use that environment when it can be used. As a result, larger populations are maintained, and the birds are a major influence on the structure of the Mugu Lagoon estuarine ecosystem without being obviously subject to its constraints.

In contrast, Mugu Lagoon may be for the fishes what the Arctic is for the birds: much better than the adjacent ocean for survival and growth of young during the summer but worse in the winter. Probably the lagoon is at its most inhospitable for fishes during major winter storms because of temporarily low salinity, high turbidity and occasionally widespread mortality of invertebrates; however, the prevalence of fish-eating birds could be a major factor as well. If predation by birds is responsible for much of the 20% per month losses suggested by population changes in the summer (Figure 47), fish might have ample cause to vacate the lagoon in winter, when the fish-eating birds are even more abundant (Figure 38). Whatever the cause, catches were an order of magnitude less in December, January, and February

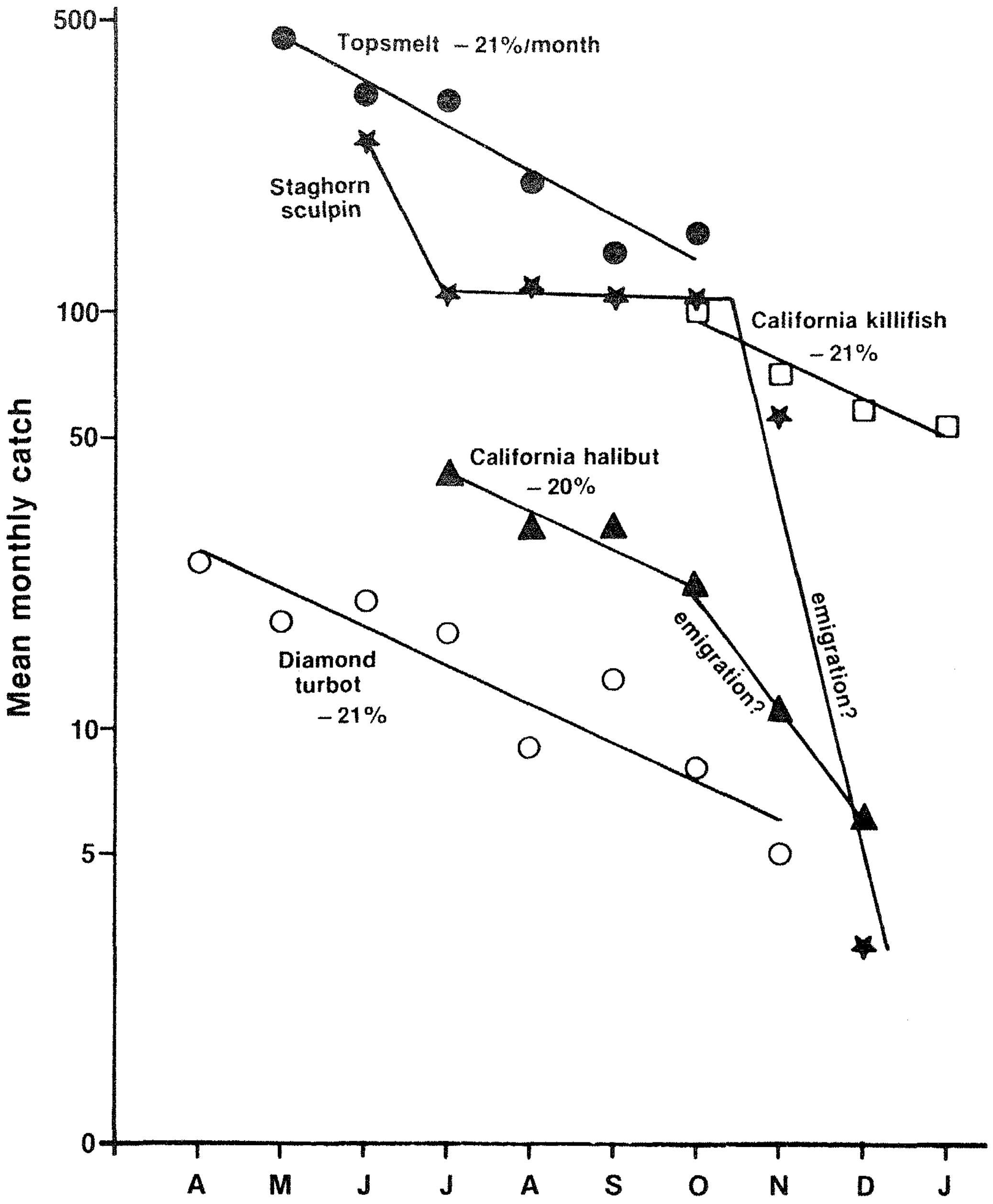


Figure 47. Monthly changes in fish abundances in the eastern arm of Mugu Lagoon after the month of peak abundance for five of the common species. Based on the 5-year means for all stations combined.

than they were in June, the month of peak abundance (Figure 35).

In the summer, three factors probably make the lagoon superior to the adjacent ocean as an environment for fish (at least small fish): (1) Food is abundant, (2) Predators are relatively scarce, (3) Temperatures are high (see Chapter 2). Except for temperature, comparable data for adjacent coastal waters are not available; however, invertebrate abundances are unlikely to be as dense outside as inside, and large piscivorous fish certainly are present outside the lagoon but almost never inside. Lower predation on early stages will allow a higher proportion of a population to survive these vulnerable life stages. Higher food densities will increase growth rates. Higher temperatures will further increase the rate of growth and development. Individuals may be larger than they would be without their stay in the lagoon. Presumably they will be less vulnerable to many kinds of predators in coastal waters because of their larger size. They may also survive a period of low food better.

In Mugu Lagoon less than 1% of the fish caught are greater than 20 cm long (Onuf and Quammen, unpubl. data). The only relatively common species caught as large individuals is the shovelnose guitarfish (Rhinobatos productus), a fascinating special case described at the end of this section. The ten most common species account for over 98% of the total catch and use the lagoon to varying degrees. The California killifish (Fundulus parvipinnis), diamond turbot (Hypsopsetta guttulata), longjaw mudsucker (Gillichthys marabilis), and bay pipefish (Syngnathus leptorhychus) are permanent residents. Topsmelt (Atherinops affinis) spawn in the lagoon, frequently are found there as adults, and intensively use the estuary as young of the year, but perform these activities in the nearshore ocean as well. The shiner surfperch (Cymatogaster aggregatus) visits the lagoon briefly to bear live young, and the newborn stay there briefly before returning to the ocean. The four other common species - staghorn sculpin (Leptocottus armatus), California halibut (Paralichthys californicus), California tonguefish (Symphurus atricauda), and speckled sanddab (Citharichthys stigmaeus) - are found in the lagoon as young-of-the-year individuals, almost exclusively.

Mugu Lagoon can be considered a nursery of sorts for six of the ten species that are most frequently caught there (Table 11). Although the benefits may be great for the individuals involved, the sizes of the stocks in nearby coastal waters probably are very large in proportion to the numbers that the lagoon might contribute. For instance, when a small mesh trawl was used, California tonguefish and speckled sanddab were the third and first most commonly caught fish in a 4-yr survey of Santa Monica Bay, an open water coastal area 40 km southeast of Mugu Lagoon. Topsmelt, shiner surfperch, and staghorn sculpin are common in a wide variety of nearshore environments (Fitch and Lavenberg 1975). Mugu Lagoon is the only coastal wetland with as much as 1 km^2 of subtidal habitat along 400 km of coast between Morro Bay in San Luis Obispo County and Anaheim Bay in Orange County. The corresponding area of continental shelf is almost 5,000 km^2. Even though young of the year of these species are concentrated in Mugu Lagoon and other much smaller coastal wetlands, it is hardly conceivable that the estuaries contribute significantly to the total stocks.

The California halibut is a notable exception. Recently, the nearshore environment of northern San Diego County was sampled intensively and systematically enough to provide a good understanding of the life history of the California halibut (Plummer et al. 1983). The data showed a distinct segregation by age and size according to depth. The smallest individuals were found at the shallowest depth sampled (mean length 23.5 cm at 6 m deep), and size increased consistently with depth (to a mean length of 39 cm at 30 m deep). The smallest individuals were in their second year of life, and sampling from the beach revealed no concentration of smaller halibut. In contrast, only 26 of the 1,285 halibut caught in 5 years of sampling at Mugu Lagoon were as large as 20 cm. Based on size-frequency relations in different months, at least 80% of the halibut caught in Mugu Lagoon were in their first year of life (Onuf and Quammen, unpubl. data). In this instance, it would appear that Mugu Lagoon not only serves a nursery function for a coastal fish stock, but that the stock might be obligately dependent on the lagoon and similar embayments in the region at one stage of its life cycle. This has particularly important ramifications, because the California halibut is the only species commonly using the lagoon that also supports an important commercial and sport fishery.

Shovelnose guitarfish use the lagoon in a very unusual manner. Unlike any of the other species common in the lagoon, they

Table 11. The utilization of the eastern arm of Mugu Lagoon by the 10 most commonly caught fish species in 5 years of sampling (Onuf and Quammen 1983; see also Figure 35).

Species	Rank order by abundance in total catch	Use of Mugu Lagoon	
		Permanent residence	Use consistent with a nursery function
Topsmelt	1		Large adults spawn in early spring, small adults spawn in summer, young of year reach catchable size in autumn.
Shiner surfperch	2		Adults give birth in the lagoon and leave, young stay only briefly.
Staghorn sculpin	3		Only young of the year present in the lagoon.
California killifish	4	x	
Californa halibut	5		Young of year predominant in the lagoon (>80%).
Diamond turbot	6	x	Apparently, adults only leave the lagoon briefly to spawn and die.
Longjaw mudsucker	7	x	
Bay pipefish	8	x	
California tonguefish	9		Only young of year present in the lagoon.
Speckled sanddab	10		Only young of year present in the lagoon.

are found in the lagoon only as very large adults (Onuf et al. 1979; DuBois 1981). Several hundred individuals enter the eastern arm of Mugu Lagoon in April each year, where they congregate in dense groups for several months and then depart in September. Of 370 different individuals caught in 1979, 335 were females (90%) and were much larger than individuals typically encountered offshore (Baxter 1974). Of 335 females tagged in 1979, 136 were recaptured in less intensive sampling over the next 2 years. Almost all females were carrying developing embryos; however, the embryos were fewer and much larger than reported for pregnant females caught offshore. Finally, the guts of all females examined were virtually empty, regardless of time of capture, nor were any effects of predation detectable in an exclosure experiment run where the guitarfish were observed most frequently.

The guitarfish, then, does not use the estuary either as a haven for its young or as a feeding ground. The explanation for its puzzling behavior may be that the higher summer temperatures in the lagoon than in the ocean are beneficial or even necessary for the development of embryos (Onuf et al. 1979). Observations of distribution and movement of shovelnose guitarfish were consistent with the hypothesis that they were in the lagoon during the summer to take advantage of higher water temperatures there (DuBois 1981). Temperatures were higher inside the lagoon than immediately outside, and within the lagoon the guitarfish shifted from shallow areas in the day to deeper areas at night in accordance with higher water temperatures (Section 2.4). However, no information is available on whether the rates of development of embryos are temperature- or size-dependent.

5.6 NUTRIENTS

Since no research on nutrient supply, availability, utilization, or cycling has been conducted in Mugu Lagoon, features of the nutrient regime must be inferred from other characteristics of the ecosystem. Consequently, consideration of nutrients has been deferred until most of the other information about the ecosystem has been presented, and the discussion is necessarily speculative.

The major sources of nutrients to the primary producers of the estuarine ecosystem are inputs from the watershed carried primarily by freshwater, inputs from the ocean carried by tidal movements of coastal waters, and regeneration of nutrients from the organic matter produced within the system or by organisms moving into the estuary. Much of the high biological productivity of other estuaries is attributed to the nutrient subsidy from freshwater input. The climate of the region and the geometry of Mugu Lagoon act to reduce any nutrient subsidy from the watershed. Precipitation (Figure 5b), streamflow (Figure 7), and consequently the potential for freshwater inputs to the estuary are concentrated in the coldest (Figure 5a), darkest (Figure 9) months when the smallest amount of photosynthetic biomass is present (Figures 24, 26, 29). Thus, the timing of freshwater inputs is when the ability for uptake by plants is lowest. In addition, since the long axis of the lagoon is perpendicular to the inlet stream, and the mouth of the lagoon is immediately opposite the mouth of the stream (Figure 10), the freshwater and its load of nutrients bypass most of the ecosystem altogether.

Nutrient inputs to Mugu Lagoon from the ocean may be low too. Characteristically, the waters of the continental shelf sustain much higher levels of primary production than oceanic water. In the vicinity of Mugu Lagoon, the shelf is narrow (5 - 15 km), and a submarine canyon cuts across most of it, so that the water is 180 m deep only 2.5 km from the mouth. The clarity of water that enters Mugu Lagoon on rising tides indicates that the water comes from this canyon much of the time.

The remaining major nutrient inputs for primary producers in Mugu Lagoon result from the activities of consumers. The same physical and microbial processes that break down macrophytes into detritus in interactions with primary consumers are responsible for most of the regeneration or fixation of nutrients as well. The large number of seals and birds that use the lagoon as a resting place but feed in other shore or aquatic environments (Chapter 4) could import substantial quantities of nutrients into the lagoon. Both of these sources are concentrated in subtidal areas and intertidal flats.

In many coastal wetlands, high biomass and production of salt-marsh plants are associated with ample tidal flushing. In Mugu Lagoon, low biomass and production of salt-marsh plants are characteristic of the well-flushed eastern arm, while salt-marsh vegetation is denser, taller, and more luxuriant in the well-flushed western arm (pers. observ.). This may be due to a combination of both less flooding by saltwater and higher freshwater input and nutrient enrichment from sources in the watershed. An additional explanation of the difference may be that nutrient-poor oceanic waters are sapping the salt marsh of its nutrients in Mugu Lagoon, while richer coastal waters provide a nutrient subsidy to salt marshes in many other areas. No measurements of dissolved materials have been made to determine nutrient fluxes; however, the virtual absence of a litter layer in the marshes of the eastern arm suggests that particulate matter is rapidly removed. Consequently, the nutrients regenerated by decomposition of marsh litter are first made available and probably used in other environments, such as the intertidal flats and subtidal areas of the lagoon. Presumably, more of the litter decomposes in place in the western arm. Where allochthonous nutrient inputs are low, proximity to regenerated nutrients would then result in higher biomass and production.

According to this conceptual model of the nutrient regime of Mugu Lagoon, all inputs to the salt marsh are small in the eastern arm, whereas at least nutrient regeneration, and perhaps imports by animals that feed outside the lagoon, considerably augment the availability of nutrients to primary producers in subtidal areas and on intertidal flats. Thus, nutrient availability could account for the finding of Onuf et al. (1979) that salt-marsh productivity in the eastern arm of Mugu Lagoon was low compared to other sites at similar latitudes, while benthic microfloral productivity was similar. Although the few available observations are consistent with our contention that allochthonous nutrient inputs are low and the importance of regenerated nutrients for plant growth is correspondingly high, all interpretations about the nutrient regime of Mugu Lagoon are untested hypotheses.

5.7 AN ECOLOGICAL OVERVIEW

The diversity of biotic interactions in the Mugu Lagoon estuarine ecosystem is truly immense. Earlier we alluded to the variety, steepness, and variability of the physical gradients that intersect within estuaries to account for their biotic richness. In this chapter we have examined in detail how organisms in the same and different trophic levels interact with sometimes subtle differences in the physical environment to produce different outcomes. These specific case histories and the more general patterns extracted from them provide the fullest appreciation of how the ecosystem actually functions; however, the detail is overwhelming. It precludes obtaining a sense of the structure of the whole. Here we summarize only the most prominent features of each trophic level.

Total primary production is relatively similar across the major physiographic units of the estuarine ecosystem, from subtidal areas and intertidal flats through all but the highest part of the salt marsh. However, primary producers differ enormously in structural characteristics, especially between the salt marsh and the more frequently flooded areas. In contrast, the activities of the primary consumers are heavily concentrated in and on the tidal flats and in subtidal areas. The feeding activities of the predators are necessarily confined to the same areas.

The substrate of tidal flats and subtidal areas is close to planar but soft, and the vegetation is short. Most large primary consumers are buried. Small primary consumers are buried or hidden in the vegetation. Predators are abundant. Perhaps the limits on the size or position of the primary consumers are imposed in part by the predators. Certainly, the only place to hide for anything larger than a few millimeters is in the soft bottom, not on its flat surface. Within the marsh, neither small size at the surface nor hiding in the sediment is compatible with the relatively long periods of aerial exposure alternating with relatively brief periods of submergence. Feeding time may be too short, and desiccation may be too severe.

The small or buried primary consumers that are limited in distribution to intertidal flats and permanent open-water bottoms cannot consume most of the primary production of the ecosystem as live material. Most macrophytes are unavailable because of physical separation (in the salt marsh or above the bottom) or refractory biochemical makeup. Consequently, most of the primary consumers are dependent on the same food: small particulate organic matter consisting of live microalgae and detritus produced by partial decomposition of macrophytes.

The dependence of most of the primary consumers in the Mugu Lagoon estuarine ecosystem on the same food has major repercussions for the organization of the primary consumer trophic level. Since the scope of niche differentiation according to food type is so limited, either few species of primary consumers might be expected, or criteria other than food are likely to be important in accounting for the variety of primary consumers actually present. As described above, a great diversity of physical environments can occur in an estuary. Therefore, it is hardly surprising that spatial relations prove to be very important among the primary consumers, and that an impressive diversity results. In any small area, different primary consumers will be in the water column, on the surfaces of plants, on hard surfaces, on loose sediments, or at different depths in the sediments. Those species studied that coexist within the same narrowly defined spatial environment interact strongly, and thus, tend to be separated horizontally. Physical interference commonly is the mechanism by which one species excludes another within the same stratum. Species in different strata have little demonstrable effect on each other, even though they consume the same kind of food.

A greater variety of food is available to the predators than to the primary consumers, and this is reflected in greater differentiation of diets. Nevertheless, spatial relations continue to be very important, often not correlated with the distribution of prey. Thus, neither substrate texture (over broad limits) nor the distinction between intertidal flats and adjacent subtidal areas appear to influence the polychaete prey of shorebirds (directly), but both are critical factors in determining the effect of the shorebirds.

The outstanding characteristic of the top predators is their timing. Whereas considerable feedback between trophic levels was evident lower in the food web (primary consumers eat plants, consumers regenerate nutrients for plants), the predators operate outside the control of other trophic levels within the ecosystem by migrating. This allows much heavier exploitation of food while predators are present than would be possible if they were dependent on the lagoon all of the time. The periodic relaxation of predation and recovery of prey populations has the effect of increasing the likelihood of an abundant food supply at the beginning of the next period of residence.

CHAPTER 6. COMPARISONS

6.1 GEOGRAPHIC VARIATION IN COASTAL CLIMATE AND TOPOGRAPHY

The principal natural characteristics of the coastal regions of the United States that most influence estuarine ecosystems are coastal topography, the amount and timing of precipitation, temperature, and sunlight. For its entire length, the Pacific coast is very steep, with small coastal watersheds (except for northern San Francisco Bay and the Columbia River, into which are funneled waters from extensive areas of high elevation inland of the Coast Range) (Figures 1, 48a). The continental shelf is narrow. Precipitation is heavily concentrated in the coldest months of the year and increases northward from 26 cm per year at San Diego, California, to greater than 250 cm in three coastal locations between the Oregon-California border and the northern tip of the Olympic Peninsula (Figure 48b). The timing of river runoff is closely correlated with precipitation, except in the drainages of the Columbia River and northern San Francisco Bay, where much of the precipitation is stored as snowpack and released much later (Figure 48b). The growing season is long along the whole coast (Figure 48c), but the Pacific Northwest receives one-third less solar radiation than southern California (Figure 48d), and evaporation is less than one-half (Figure 48e).

With the exception of similar south-north gradients in solar radiation and evaporation (Baldwin 1974) and the rugged topography of New England, the natural characteristics of the other coastal regions of the United States that influence estuarine ecosystems differ drastically from those just described. Most importantly, precipitation is greater than 100 cm per year from eastern Texas to the Canadian border and even southern Texas received at least twice as much precipitation as southern California (Baldwin 1974). Furthermore, the precipitation is either concentrated in the warm months or evenly distributed throughout the year. River runoff is maximal in the spring and remains substantial through midsummer (van der Leeden 1975). A long series of barrier islands buffer the effects of the open ocean on inner coastal waters. Here the whole coastal region behind the barrier islands is an estuarine ecosystem. The continental shelf is broad from Mexico to Canada, and the coastal plain is broad from Mexico to New York. By opening onto broad expanses of shallow coastal waters, eastern estuaries are linked to a greater extent than is possible on the Pacific coast.

The net effect of these factors in southern California is as described in detail for Mugu Lagoon. Estuaries here are small and discrete, separated from others by sometimes long distances of open coastal waters with a strong oceanic influence, rather than shallow water lying above a broad continental shelf. Precipitation and river runoff, including the river's supply of nutrients, virtually cease before the period of high plant growth in May through August; at the same time, evaporation rates are high. The combination of low nutrient supply and high and increasing soil salinities when maximal growth should be occurring probably reduce the productivity of the fringing marshes considerably compared to what otherwise might be possible. These constraints on plant growth do not exist on tidal flats and in subtidal areas. However, the virtual absence of a salinity gradient during most of the year restricts some uses of

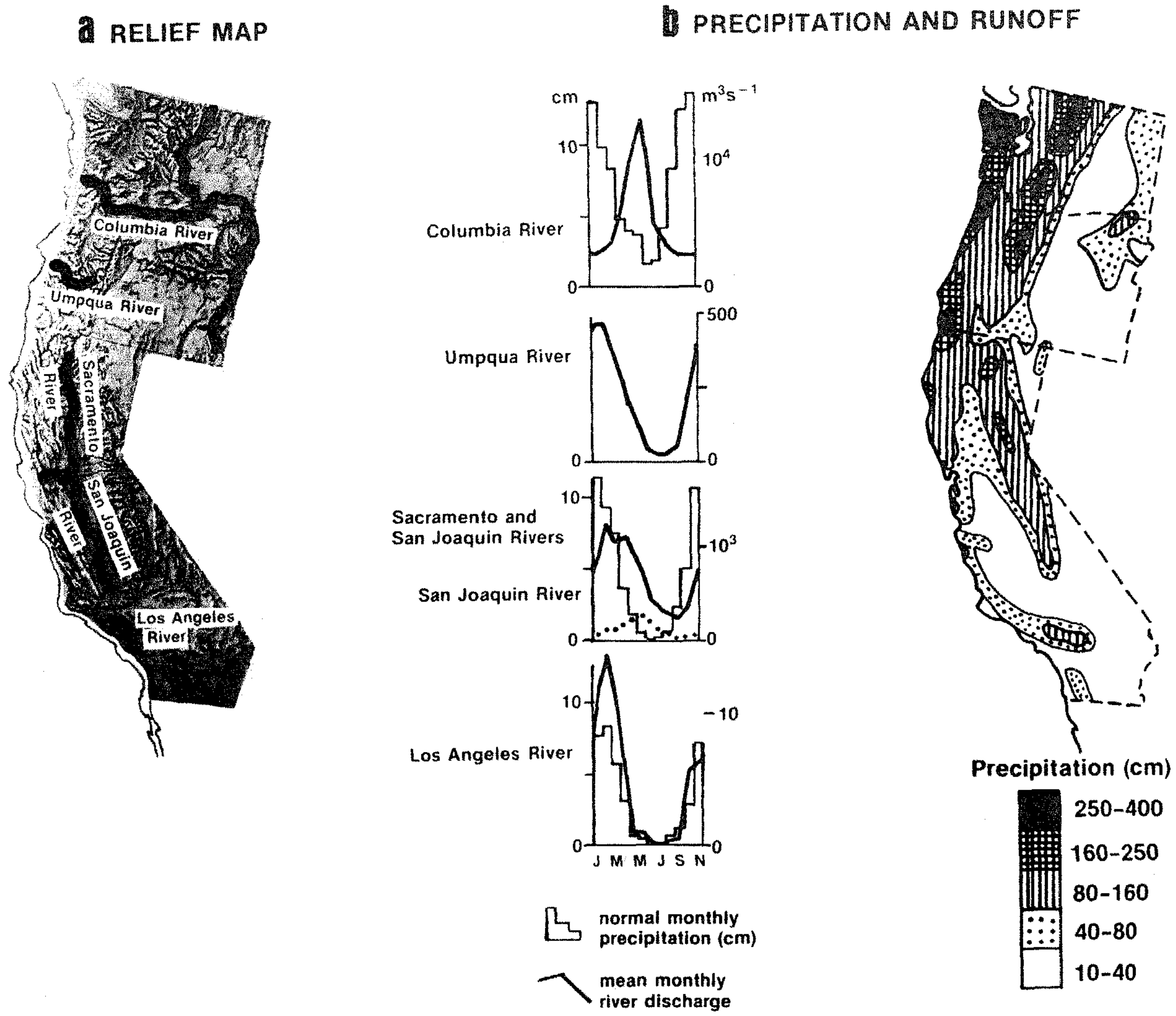
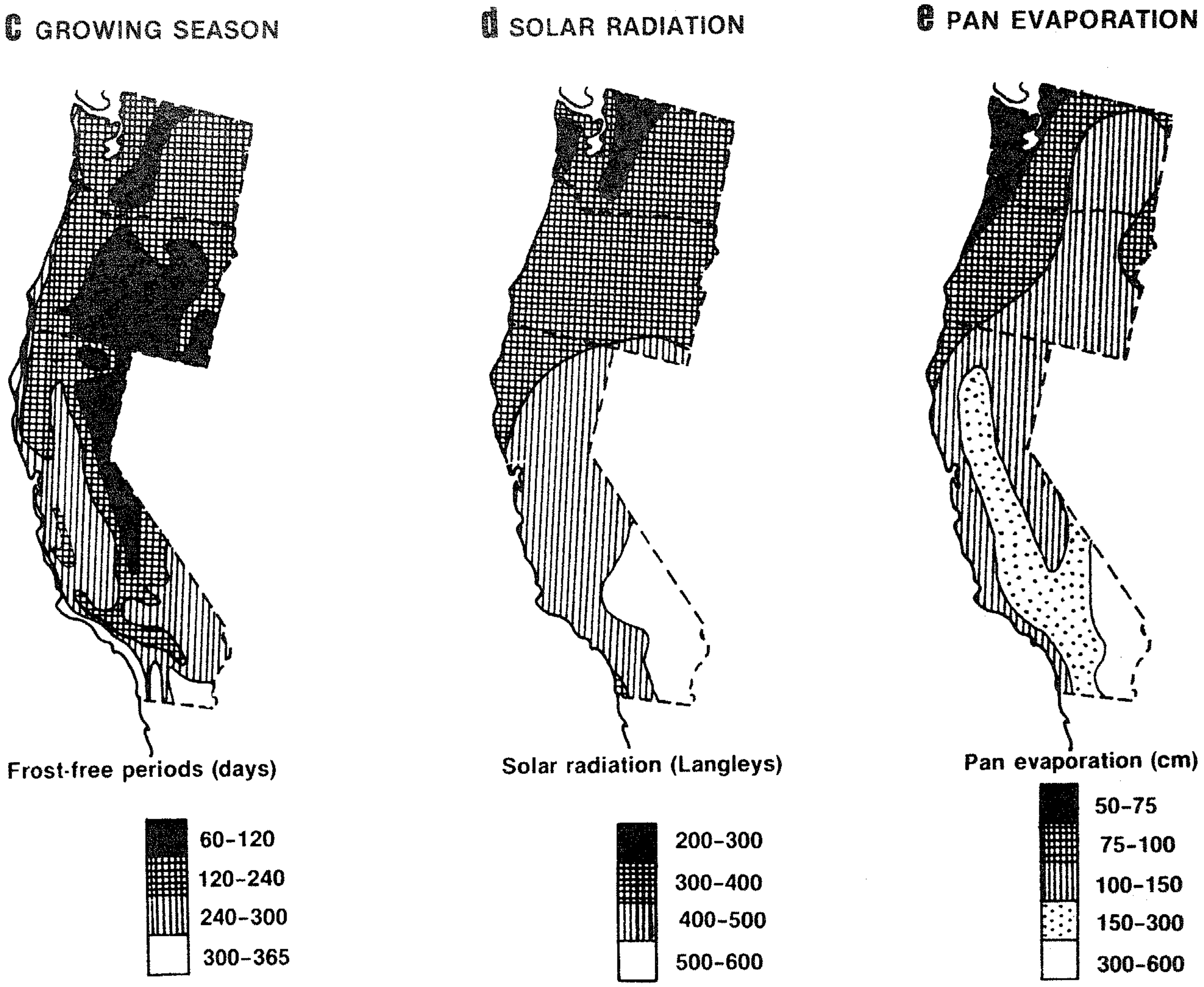


Figure 48. The Pacific coast of North America from 30° to 50°N. (a) Physical relief, showing the rugged topography of the coastal region and the narrow continental shelf. (b) Normal monthly total precipitation (cm), mean monthly river discharge (m^3/s) for

the estuary and the presence of some kinds of organisms. Most importantly, no refuge from natural enemies is available through differential tolerance to low-salinity waters, one imputed source of the high value of estuaries as nursery areas for some species (Douglas and Stroud 1971).

Despite a somewhat similar topography, the climatic differences of the Pacific Northwest lead to differences in estuarine functioning. Since evaporation is much less than in the south (Figure 48e), stressful soil salinities are less likely, but less light (Figure 48d), lower temperatures, and maximal plant growth out of phase with nutrients supplied by river runoff, as in the Pacific Southwest, suggest that the productivity of the salt marshes may not differ appreciably in the north. Since river runoff does not cease altogether in the summer (Figure 48b), an enhanced nursery function is possible compared to the south, but the rugged topography still assures that the estuaries are small and discrete.



different drainages, and mean annual total precipitation (cm). (c) Growing season (frost-free period in days). (d) Mean daily solar radiation (Langleys). (e) Mean annual pan evaporation (cm). (a-adapted from U.S. Geological Survey 1974; b to e-Baldwin 1974; b-Kahrl 1978 and van der Leeden 1975.)

As noted previously, the biological characteristics of northern San Francisco Bay and the Columbia River estuary are not constrained by the timing of freshwater input, which occurs in spring and summer when reduced salinity would contribute most to plant growth and use of the estuaries by juvenile stages of fish and invertebrates.

On the east coast, topographic factors greatly expand the influence of estuarine conditions. In addition, the timing of precipitation and river runoff coincide with the period of maximal plant growth. Therefore, stressful conditions of soil salinity are minimized, and nutrients from terrestrial sources are made available to marsh plants at the most appropriate time.

This suggests that the increases in the length of the growing season and the amount of solar radiation from north to south will result in relatively high productivity of salt marsh plants in the north and very high productivity in the south, compared to other regions. The shorter growing season (frost-free period) of New England, as compared to the Pacific Northwest (Baldwin 1974), may result in somewhat lower productivity of New England salt marshes, but the difference in the length of the growing season is partly compensated by very low light early in the growing season and low temperature at the peak of the growing season in the Pacific Northwest. The nursery function is great by all criteria, including some not discussed in the rest of this inter-regional comparison: abundant food supplies, high temperature, and protection from natural enemies.

Despite similar long growing seasons and solar radiation, the productivity of salt marsh macrophytes is much lower in the arid Southwest than in the moist Southeast (Zedler et al. 1978; Onuf et al. 1979; however, also see Eilers 1981). South to north gradients in salt marsh productivity on the two coasts also point to an important effect of the lack of freshwater input to account for the conditions observed in southern California. On the Atlantic coast, where freshwater input varies little from the southernmost tip of Florida to the Canadian border (Baldwin 1974; van der Leeden 1975), a strong decreasing gradient in productivity with increasing latitude has long been recognized (Turner 1976). In contrast, on the Pacific coast, where precipitation increases from less than one-fourth of that of the Atlantic coast near the Mexican border to substantially more than anywhere on the Atlantic coast from northern California to the Canadian border, salt-marsh productivity decreases little, if at all, at least from southernmost California to central Oregon (Macdonald and Barbour 1974; Onuf et al. 1979; Eilers 1981; Josselyn 1983; Seliskar and Gallagher 1983). This suggests that greater freshwater input might be compensating for lower light and temperature going northward on the Pacific coast.

Zedler (1982) stated well the reasons to believe that the high soil salinities of the long summer drought period are responsible for limiting growth and productivity in southern California salt marshes; however, the observations presented above do not distinguish whether another consequence of little freshwater input during the growing season is nutrient limitation of growth. Nor do those observations test the imputed importance of timing. As it stands, we can be quite certain that freshwater input is an important determinant of how salt marshes function in southern California and the most important determinant of differences between salt marshes in southern California and other regions of the United States. The mechanism behind this, however, is unknown.

6.2 COMPARISON OF MUGU LAGOON TO THE OTHER SOUTHERN CALIFORNIA ESTUARIES

The great variety of coastal wetlands in similar natural environmental settings in southern California has three obvious causes: size, connection with the ocean, and man-caused alterations. Perhaps most important is that the setting is no longer natural (Zedler 1982). Probably every estuarine ecosystem in southern California has undergone major alterations as a result of human activities. Portions of many have been dredged to provide ports and marinas, while other portions have been filled to provide airports and space for real-estate development. Marshes have been diked for a multitude of reasons, ranging from exploitation of petroleum reserves to management of waterfowl populations. Channels have been deepened and realigned, primarily for flood control and navigation. Highways and railroads have been built across most coastal wetlands, perhaps pre-empting little area, but always altering circulation and often restricting the location of the mouth. Dams have been built on many of the inlet streams, intercepting sediments, diverting water, and altering the timing of water delivery to the estuary. Land-use practices, particularly agriculture, have accelerated erosion and, through drainage of water used in irrigation, altered the timing of the delivery of water to estuaries.

The other two factors, size and communication with the ocean, undoubtedly led to great differences among estuaries under natural conditions, but also are affected by human modifications. The physical environment (Carpelan 1969), the floras and primary productivity (Zedler 1982), and the faunas (Mudie et al. 1974) are very different depending on the frequency, timing, and duration of a surface-water connection between the estuary and the ocean. The reason that estuaries differ in their water connections to the ocean is that the longshore drift of sand (described in Chapter 3 in the context of inlet migration) happens almost all of the time and tends to fill in any opening to an estuary. Unless sufficient flow into or out of the estuary counteracts this filling, the mouth will close. The two sources of flow are tidal currents and river or creek discharge. Estuaries with a large area subject to tidal change in depth will always remain open, hence the importance of the size of the estuary. Somewhat smaller estuaries may be open most of the time, but, once closed, probably require the winter high flow of inlet streams to reopen them. Smaller estuaries will differ among themselves and within and between years, depending on their relations to freshwater sources. They can range from being fresh almost all of the time to being brackish at the time of closure and then becoming hypersaline as evaporation proceeds.

Detailed comparisons are possible for some important features of structure and function between Mugu Lagoon and three other small southern California estuarine systems: Anaheim Bay, Upper Newport Bay, and Tijuana Estuary (Figure 49). Although all have been modified by human activities, they have in common continuous, or close to continuous, connections with the ocean, relatively large size by regional standards, a variety of little-disturbed subtidal and intertidal habitats, and natural associations between most habitats (for instance, broad flats between emergent marsh and shallow open water). Comparisons among these estuaries test the validity of the analysis of estuarine ecosystem function developed in this profile, based on Mugu Lagoon alone, and extend the analysis to situations not specifically studied in Mugu Lagoon.

Tijuana Estuary (Figure 49b) is the only site in southern California besides Mugu Lagoon where an integrated effort has been made to assess the contributions of different sources of primary production (Zedler et al. 1978; Zedler 1982). The two systems are similar in the relatively low productivity of the vascular plants of their salt marshes (compared to other regions) and the proportionately great contribution of the benthic microflora to total production. The two systems differ in the virtual absence of Spartina from Mugu Lagoon and its domination of the lower marsh at Tijuana Estuary, the very low productivity of vascular plants in the lower marsh at Mugu Lagoon, and in the relatively broad continental shelf contiguous to Tijuana Estuary, rather than the narrow shelf cut by a submarine canyon as at Mugu Lagoon. Although dredging eliminated most of the cordgrass that once was present in Mugu Lagoon (Macdonald and Barbour 1974), this activity did not affect the areas studied in the eastern arm. There, the absence of major freshwater inputs until recent times, and the short duration of these inputs even now, probably preclude the establishment of cordgrass, because germination and early growth appear to require reduced salinities (Zedler 1982, pers. comm.).

In Chapter 5, the submarine canyon cutting across the already narrow continental shelf at Mugu Lagoon (Figure 13b) was hypothesized to deliver nutrient-poor oceanic water into the lagoon during tidal exchange to account for the low productivity of the marsh in the well-flushed eastern arm. Instead, Tijuana Estuary (Figure 49b) is flushed by water from a much broader segment of continental shelf and consequently may be richer in nutrients. The twofold difference in low marsh productivity between the two estuaries (Figure 50) is consistent with this presumed difference in their nutrient regimes.

Six species accounted for 94% of all shelled macroinvertebrates collected by Peterson (1975) during 3 years of sampling in the sandy subtidal areas of Mugu Lagoon (Table 12). The same six species accounted for 83% of all individuals collected in similar habitats at Tijuana

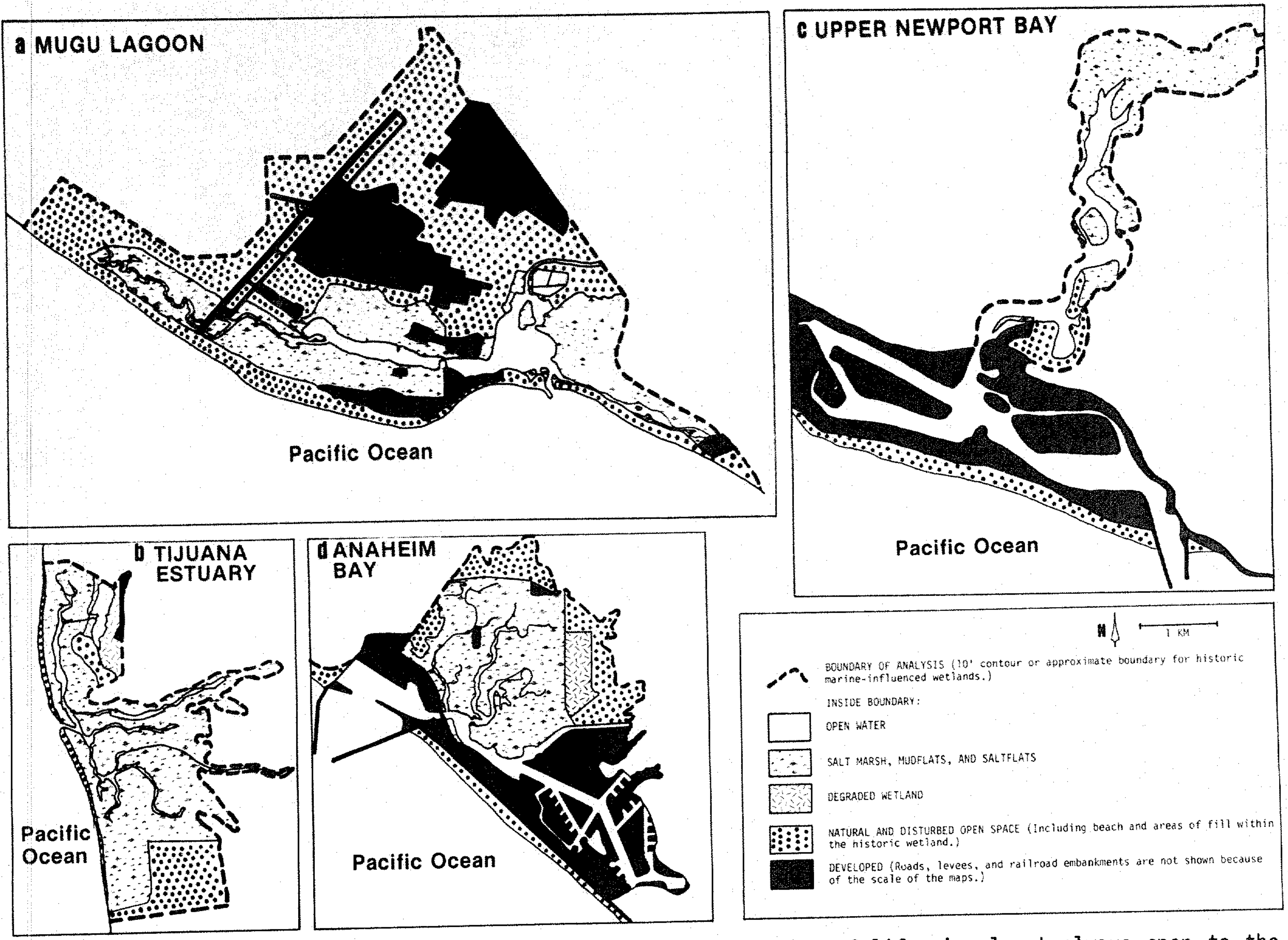


Figure 49. The large (by regional standards) estuaries of southern California almost always open to the ocean, with relatively large areas of remaining natural habitats, and natural connections between habitats within the estuarine system. (a) Mugu Lagoon, (b) Tijuana Estuary, (c) Upper Newport Bay, (d) Anaheim Bay.

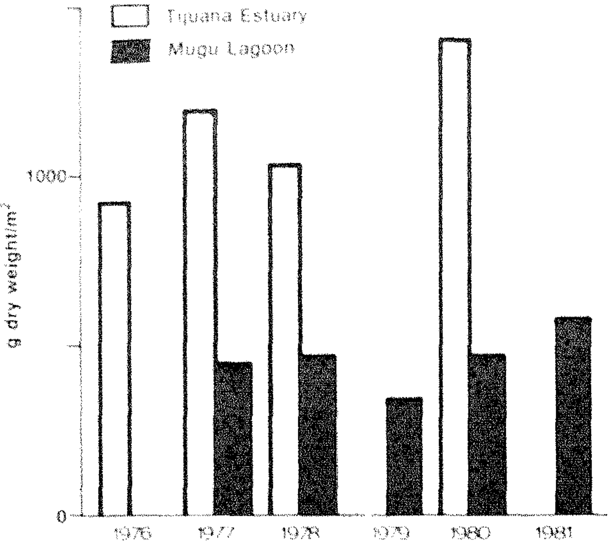


Figure 50. Primary productivity as measured by August biomass of the lower marshes at Tijuana Estuary (from Zedler 1982) and Mugu Lagoon.

Estuary during the same period. However, the two most common species at Mugu Lagoon (the commensals *Callianassa californiensis* and *Cryptomya californica*) were very rare at Tijuana Estuary. During the study of the invertebrates, an active bait fishery for the ghost shrimp *Callianassa* was in progress, using pumps powered by gasoline engines to flush *Callianassa* out of its burrows (Peterson 1972). Of course, the removal of *Callianassa* also doomed its commensal, the clam *Cryptomya*. There were greater densities of deep-dwelling *Nuttallia* and *Tagelus* (in the same stratum of the sediments as *Callianassa* and *Cryptomya*), coupled with only slightly lower densities of shallow-dwelling *Protothaca* and *Dendraster* at Tijuana Estuary compared to Mugu Lagoon. This pattern is consistent with Peterson's (1977) hypothesis that competition for space is instrumental in determining the structure of this benthic community, and that biological interactions are strongest within the same depth stratum (see Chapter 5).

Table 12. The mean densities (number/m²) of the common shelled macroinvertebrates and their percent of total density in subtidal sandy areas of Mugu Lagoon and Tijuana Estuary sampled at 4-month intervals between July 1969 and July 1972 (adapted from Peterson 1975). C = crustacean, E = echinoderm, no notation = bivalve.

Macroinvertebrate	Mugu Lagoon		Tijuana Estuary	
	Density	%	Density	%
Cryptomya californica	273	50	2	1
Callianassa californiensis (C)	88	16	3	2
Protothaca staminea	59	11	35	19
Nuttallia (Sanguinolaria) nuttallii	47	9	76	41
Dendraster excentricus (E)	37	7	23	12
Tagelus californianus	9	2	14	8
All others	35	6	31	17
Total	547		184	

Although the methods of collection differed between locations, sufficient data exist to compare the fish faunas among the four large, permanently open, not completely artificial estuarine systems of southern California (Table 13). Mugu Lagoon, Tijuana Estuary and Anaheim Bay resemble each other closely. Topsmelt is the numerical dominant in all three wetlands, and staghorn sculpin, California killifish, California halibut, and diamond turbot are all abundant in each wetland. Probably the lack of wide expanses of permanent open water in Tijuana Estuary (Figure 49b) accounts for the rarity of shiner surfperch there. The diamond

Table 13. Ranking of abundances of common fish species in four large southern California coastal wetlands.

Species	Mugu Lagoon[a]	Tijuana Estuary[b]	Anaheim Bay[c]	Upper Newport Bay: Littoral 1974-75[d]	Upper Newport Bay: Littoral 1978-79[e]	Upper Newport Bay: Open water 1974-75[d]
Topsmelt (*Atherinops affinis*)	1	1	1	1	1	
Shiner surfperch (*Cymatogaster aggregata*)	2		4	3		1
Staghorn sculpin (*Leptocottus armatus*)	3	2	5	4		
California killifish (*Fundulus parvipinnis*)	4	3	3	2	2	
California halibut (*Paralichthys californicus*)	5	4	7			7
Diamond turbot (*Hypsopsetta guttulata*)	6	5	2			4
Arrow goby (*Clevelandia ios*)	*	*	*	*	4*	
Striped mullet (*Mugil cephalus*)		6				
Deepbody anchovy (*Anchoa compressa*)			6	5	5	
Slough anchovy (*Anchoa delicatissima*)				6		3
Mosquitofish (*Gambusia affinis*)					3	
Black surfperch (*Embiotoca jacksoni*)						2
Round stingray (*Urolophus halleri*)						5
White surfperch (*Phanerodon furcatus*)						6

[a] Onuf and Quammen (1983).
[b] White et al. (unpubl. rep.).
[c] Lane and Hill (1975).
[d] Allen (1976).
[e] Allen (1980).
*Probably much more abundant than any other species, but inadequately sampled by gear used.

turbot is relatively more common at Anaheim Bay than at the other locations, but the reasons for this are not known.

Two features distinguish Upper Newport Bay from the other locations. The bay is large enough that the fish fauna of its open-water areas is distinctly different from that of its littoral areas (Figure 49c). Surfperch and flatfish characterize the former, while topsmelt, killifish, and sculpin typify the latter. Anchovies occur in both areas. Although some of this differentiation can be detected at Mugu Lagoon (Tables 5, 6) and in Anaheim Bay (Lane and Hill 1975), the spatial separation between open water and littoral areas is rather small, and topsmelt is not a littoral species. The other distinctive feature of Newport Bay is the abundance of mosquitofish (a primarily freshwater species) in the littoral zone in 1978, one of the major storm years that figured so importantly in the analysis of ecosystem function for Mugu Lagoon. At Upper Newport Bay, shiner surfperch and staghorn sculpin were more abundant in the dry period sampled (1974-75) than the wet period (1978-79). Shiner surfperch also declined at Mugu Lagoon in the 1978-79 wet period; however, staghorn sculpin did not decline, and no freshwater fishes were caught there in the wet period. Whether both differences arise from a greater freshwater influence in Upper Newport Bay is uncertain. Eggs and larvae of staghorn sculpin in Tomales Bay, California cannot survive salinities <10 ppt, but juveniles thrive in freshwater (Jones 1962). In southern California, tolerances might reasonably be lower.

Four other southern California estuaries have mouths that are open to the ocean most of the time: Agua Hedionda Lagoon, Upper Bolsa Bay (the State Ecological Reserve), Carpinteria Slough, and Goleta Slough (Figure 51a-d), but differ from Mugu Lagoon much more than Tijuana Estuary, Upper Newport Bay, and Anaheim Bay in other characteristics. All are much smaller than Mugu Lagoon. Dredging within Agua Hedionda Lagoon (Figure 51a) has expanded the area of permanent open water greatly at the expense of tidal flats and salt marsh (Bradshaw et al. 1976). Instead of a gradual progression from salt marsh across tidal flats into shallow subtidal areas, there is an abrupt dropoff from an upland edge or salt marsh into relatively deep water. Coastal fishes not commonly associated with wetlands might be expected, while shallow-water species such as the California killifish should be relatively rare. Birds of the open water, such as grebes and diving ducks, should be abundant, and shorebirds should be rare. A long passage through a marina intercedes between the entrance to Upper Bolsa Bay (Figure 51b) and the ocean. This is bound to affect use of the wetland by fishes and perhaps is a barrier to some kinds of invertebrates. Carpinteria Slough (Figure 51c) lacks in area of open water. Over half of the open water is in the form of channels, artificially deepened and steepened for flood control and separated from the adjacent salt marsh by dikes (Macdonald 1976a). Even more of Goleta Slough (Figure 51d) is so modified, and tidal flats are virtually absent as well (Speth et al. 1970). Especially in the latter, the limited area and monotony of the permanent water habitats should result in low abundance and variety of the wetland fauna.

Los Peñasquitos Lagoon's ocean connection (Figure 51e) is very unpredictable in occurrence and duration (Mudie et al. 1974). When its mouth has been open for several months, Los Peñasquitos Lagoon probably is similar to Mugu Lagoon in ecosystem structure and function. When the mouth is closed or only recently opened, the relations described in this profile will not apply. Closure is the rule rather than the exception in most other coastal wetland ecosystems of the region. The resulting differences are too numerous for the analysis of ecosystem function in Mugu Lagoon to be relevant. Even "intermittent estuary" is a misnomer in this case.

In summary, the correspondences in many aspects of the biology of the four large open coastal wetlands of California are considerable. This provides some cause for believing that the analysis of the Mugu Lagoon estuarine ecosystem may be of more general significance. Perhaps more importantly, the differences should provide valuable checks on some of the more extravagant extrapolations required to synthesize a complete analysis for Mugu Lagoon. Furthermore, those differences should allow the extension of the basic analysis to a broader array of conditions, as outlined above.

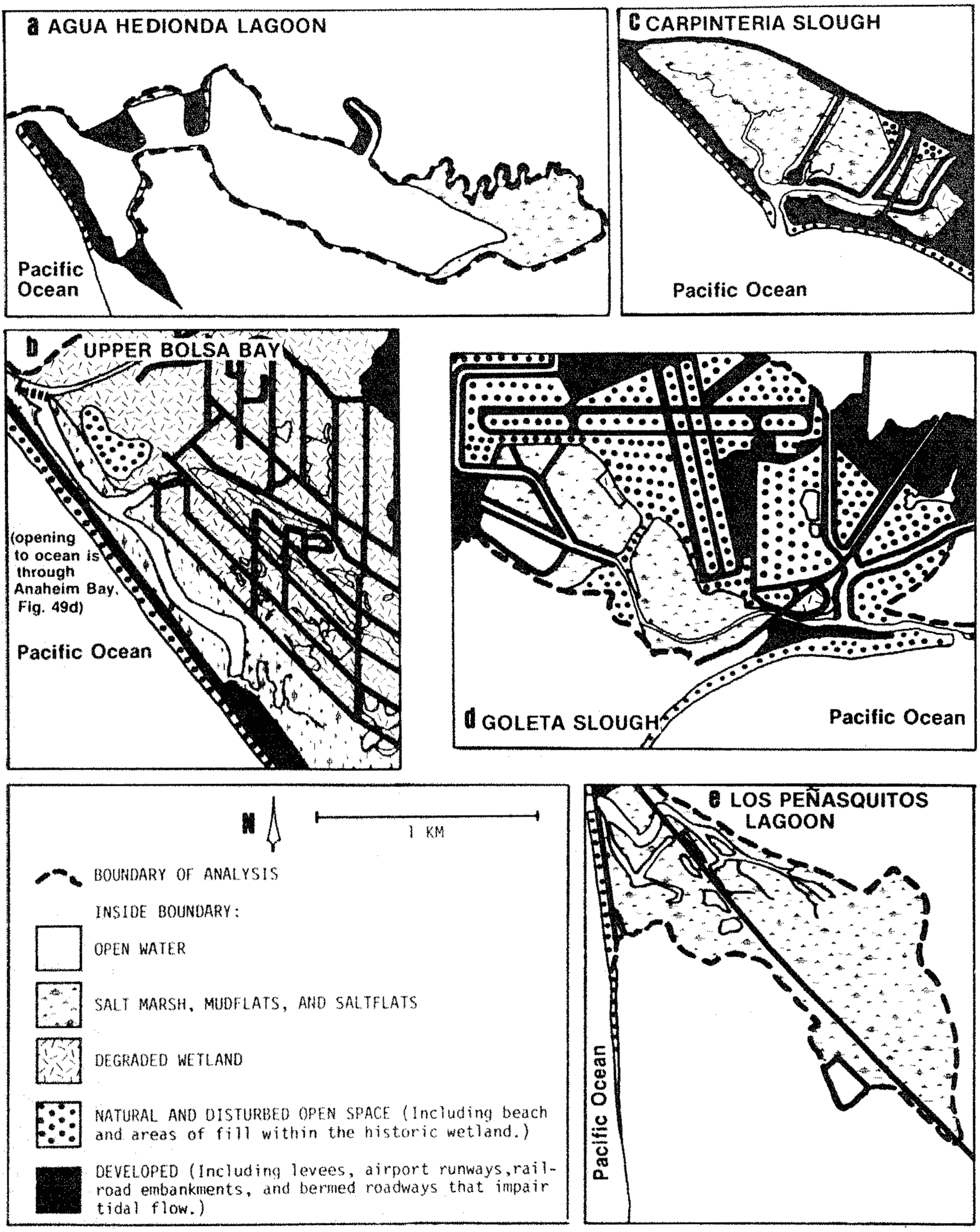


Figure 51. Smaller estuaries of southern California, always open but only indirectly connected to ocean or with altered relations between habitats within the estuary: (a) Agua Hedionda, (b) Upper Bolsa Bay (the State Ecological Reserve), (c) Carpinteria Slough, and (d) Goleta Slough; or unpredictably open to the ocean: (e) Los Peñasquitos Lagoon.

CHAPTER 7. MANAGEMENT CONSIDERATIONS

In southern California, encroachments on estuarine systems have been so severe that we cannot really know what these systems were like and how they functioned before the appearance of man in the region. In that sense, the remnants of estuaries are not "natural" (i.e., intact examples of a whole ecosystem). On the other hand, the estuarine realm where freshwater, marine, and terrestrial influences commingle always has been subject to a wider range of fluctuating inputs and conditions than almost any other ecosystem. Consequently, many of the alterations caused by human activities lie within the range of conditions experienced by the natural system. Thus, many of the remaining parts of estuaries in southern California today probably had counterparts in estuaries before human influence.

Unfortunately, the proportionate contributions of different parts of estuarine ecosystems in southern California have been altered so drastically that we can not even guess what the natural proportions might have been. Some parts or their connections to the rest of the estuarine ecosystem have been almost entirely eliminated. Functions that depended on those parts or connections inevitably have been eliminated or drastically curtailed. The most obvious of these are the elimination of most freshwater marshes, the separation of most of the remaining freshwater marshes from tidal wetlands by levees or roads and railroad embankments, and the consequent elimination of brackish water habitats. For waterfowl, part of this loss has been made good by purposeful management of impounded areas of freshwater for the enhancement of game bird populations. However, if a nursery function ever existed based on a gradual transition from freshwater to seawater, it has been lost in its entirety. Clearly, the whole is not what it once was. Nevertheless, the remainder continues to be a dense mosaic of natural habitats, all the more deserving of protection and careful management for educational, scientific, and aesthetic purposes because of their proximity to densely populated areas (Onuf et al. 1979), in addition to their incalculable primary value in support of endangered species and as habitat islands for other sensitive wildlife.

The main concerns in managing the surviving small remnants of estuarine ecosystems in southern California are protecting those remnants from the impacts they can not tolerate (for instance, high levels of sedimentation), restoring degraded areas, and responding to the needs of endangered species. The Navy's role in protecting the natural resources of the Mugu Lagoon estuarine ecosystem is summarized in the next section. Some specific concerns about management that have arisen in this report are then addressed: (1) sedimentation, (2) other water-borne contaminants, (3) alteration of tidal flushing, (4) endangered species, and (5) information gaps.

7.1 PROTECTION

Because it is enclosed by a military base, Mugu Lagoon is well protected from further development pressure. Public access to sensitive natural areas is quite restricted for military security reasons, and even scientific research requests are carefully screened by a review board to avoid potential impacts to the ecosystem. In 1963, the Navy entered into an agreement with the Fish and Wildlife Service and the California Department of Fish and Game to formulate a fish and wildlife management plan to allow and promote preservation of the ecosystem and its species assemblage. This Cooperative Plan was updated in 1976 with the adoption of a Fish and Wildlife Management Plant for the Navy base and nearby San Nicolas Island. With the recent establishment of the Santa Monica Mountains National Recreation Area, the Navy and the Park Service entered into an interagency agreement for management of the eastern arm and central basin. These parts of the lagoon are included in the National Recreation Area but remain Navy property and under Navy control.

Military management has consisted of active conservation of the natural resources of the lagoon and its wetlands, with promotion of research into the ecological structure and functioning of the lagoon and its fringing wetlands by Navy biologists and other scientists. However, much of the management of the estuary might be better termed as passive, that is, maintained in its natural state. The Navy successfully prevented opening of the barrier beaches to development in the 1960's, and continues to promote regional development consistent with minimizing impacts to the lagoon. Continued development of the watershed outside the area of military or National Park Service control poses the most probable and substantial impact to the estuary through the threat of increased sedimentation, discussed in the following section.

7.2 SEDIMENTATION

Major storms in 1978 and 1980 caused large and long-lasting changes in the morphology of the central basin and eastern arm of Mugu Lagoon. The central basin was transformed from a wide expanse of permanent open water into a predominantly intertidal area in 1978, while the mean depth at low water in the eastern arm diminished by 25%. The deepest areas decreased most in depth. In 1980, the deposition of new sediments decreased depth of low water another 17% (Figure 18). If not for the breaching of a levee on Calleguas Creek and the deposition of thousands of cubic yards of sediments on sod fields, the deposition of sediments in the eastern arm would have been considerably greater.

The relations of these physical impacts on the lagoon with characteristics of the lagoon and watershed, land use within the watershed, and the climatic cycle have been described earlier. The biological consequences of these physical changes have been a key theme through most of the preceding analysis of ecosystem function. The implications for management are stark.

In fact, the major storms that caused the alterations described in this report are not rare events. Four such storms occurred within 20 years between 1961 and 1980. Judging by the evidence for long-term hydrological cycles in the Pacific Southwest (Figure 6) and the indications that a moist period has just begun (Figure 20), it seems very likely that storms with effects at least as severe as those of 1978 and 1980 will occur in the near future.

These observations suggest that Mugu Lagoon will not persist much longer as we now know it. As the central basin and eastern arm fill further, I suspect that they will take on the form of a floodplain rather than a slough system, such as at Carpinteria and Goleta. At those locations the natural alluvial fans are at the landward extremities of the wetlands where streams once discharged, but now those streams pass through the wetlands in channels that have been artificially widened and deepened for flood control purposes. In most cases, the channels are flanked by levees, and coarse sediments are removed in debris-retention basins before entering the slough channels. Thus, most sediments bypass the sloughs.

At Mugu Lagoon, barring failure of levees upstream, almost the entire particulate load of the inlet streams discharges into the heart of the wetland. Because flood flows with their sometimes heavy burdens of suspended particulate material and bedload are not confined within a narrow channel, they will spread out, slow down, and drop some to much of the sediment that they carry, depending upon the residence time of the floodwater and interactions with seawater that cause flocculation and hasten deposition of fine particles. Therefore, rather than passing through a relatively long-lived intermediate stage resembling Carpinteria and Goleta Sloughs, where at least the salt marsh part of the coastal wetland ecosystem persists, I foresee the rapid development of an alluvial fan that engulfs the marsh as well as the lower elevations of the lagoon. Because of the artificially restricted contact between the western arm and the central basin, filling will be much slower in the western arm. According to projections of the Soil Conservation Service (1983), the only wetlands that will exist by the year 2030 will be a thin finger extending into the eastern arm and narrow corridors passing through what now is the central basin to the western arm and the termination of the channelized portion of Calleguas Creek (Figure 52).

A consequence of the central and eastern parts of Mugu Lagoon prograding into a floodplain is that the threat of flooding to the developed parts of the Naval Air Station will increase. By definition, a stream overtops its

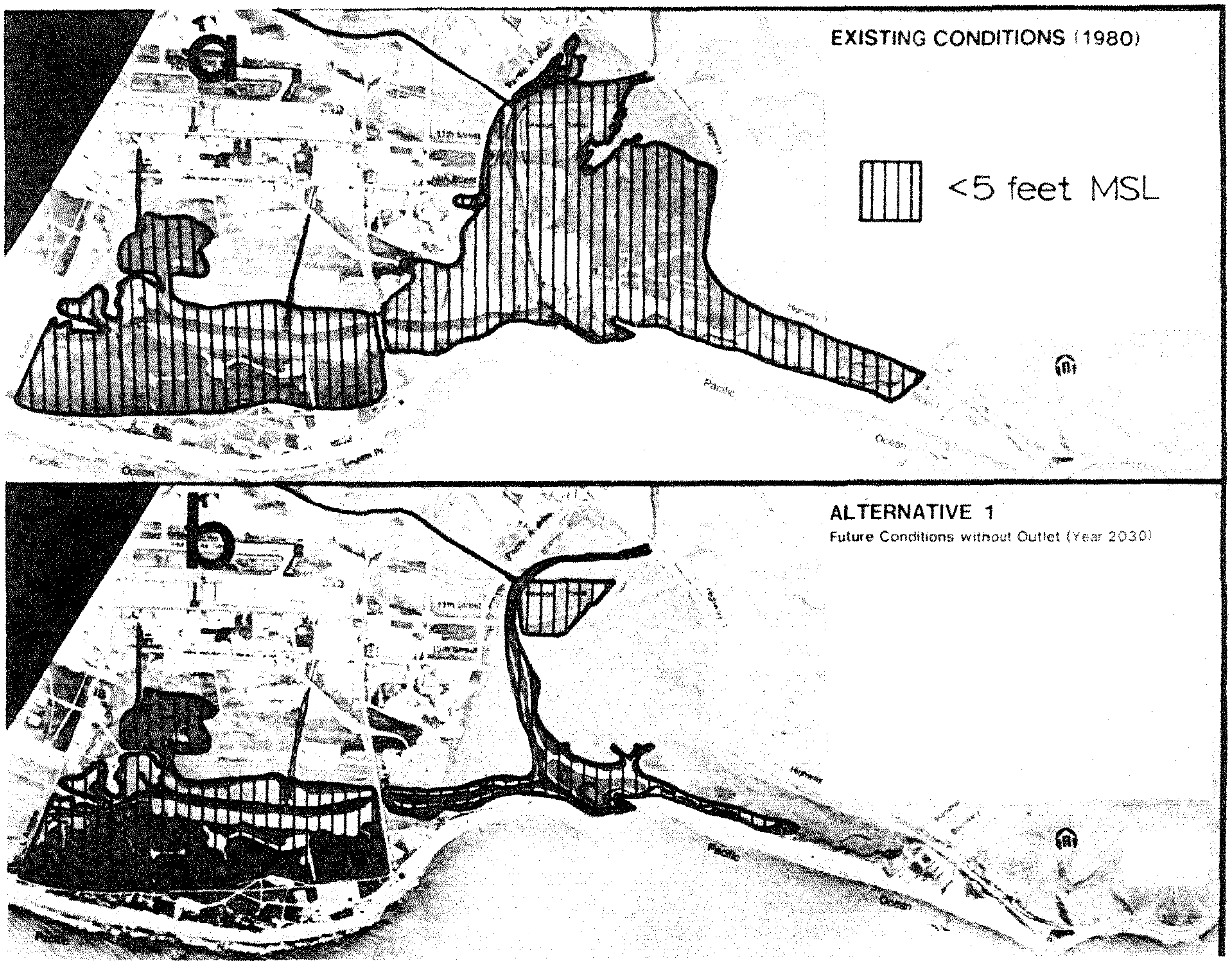


Figure 52. Topographic maps of (a) Mugu Lagoon in 1980 and (b) as projected in 2030 assuming present rates of filling continue for the next 50 years (from Soil Conservation Service 1983).

previous channel in its floodplain during major storms. When the floodplain is at elevations that exceed 5 ft (1.5 m) MSL as projected in Figure 52, adjacent developed areas at elevations <10 ft (3 m) MSL will be in jeopardy. This includes most of the facilities at Point Mugu Naval Air Station.

I infer on the basis of these considerations that channelization of Calleguas Creek will be required before the conditions described above have been realized. If future containment is inevitable, as I have just postulated, the sooner it is undertaken the better. Now relatively large and diverse areas of wetland habitat still exist in the central basin and eastern arm of Mugu Lagoon. The sooner they can be separated from the storm flows of Calleguas Creek, the bigger and the more varied the area of aquatic habitats will be that can be sustained (salvaged might be more apt) in the Mugu Lagoon estuarine ecosystem. Therefore, evaluation of options to intercept sediments upstream of Mugu Lagoon and to divert floodwaters around the lagoon (Figure 53a) should be the highest priority of management of the Mugu Lagoon estuarine ecosystem. Even channelization straight through the middle of Mugu Lagoon (Figure 53b), if done soon enough, is preferable to taking no action until flooding of the Navy base compels action.

The recommendation to preserve wetland resources by making massive structural alterations within the estuary runs so counter to any perception of natural habitat relations that it requires further explanation. The point is that past alteration of the inlet stream is the fundamental violation of natural relations. Calleguas Creek would not discharge the majority of its burden of particulate matter into Mugu Lagoon if it were not constrained to do so by artificial levees, as the breached levees of 1980 demonstrated so strikingly. The necessity for manifestly artificial measures in part of a system to redeem natural function in the remainder, albeit partial, should be evident in this context. Such was the unintended effect of the dredging of the central basin in the 1950's and early 1960's. At the expense of a big hole in the middle of the "natural" shallow water environments of the lagoon, the dominance of the marine connection was re-established in the rest of the lagoon temporarily. Unfortunately, the amount and character of subsequent development in the upper watershed probably abbreviated the lifespan of the hole considerably and compromised the utility of dredged basins here as management tools in the future.

The problem of sedimentation is the most serious concern of management in most of the coastal wetlands of southern California. Unfortunately, the sources of the problem lie far away from the affected wetlands and far beyond the authority of the agency or agencies responsible for the management of the wetlands. Certainly, much of the erosion in coastal watersheds that supplies the sediments that fill coastal wetlands is avoidable by proper zoning and instituting land-use practices appropriate to a particular geological setting. Also certainly, large benefits would be realized in the watershed as well as in the wetland if the best practices of watershed management were carried out. Fertile topsoil would be conserved, property maintenance (including roads) would be less expensive, and retention of groundwater could be enhanced.

The main obstacles to achieving these mutually beneficial outcomes are that the institutional mechanisms do not exist to implement such management programs, and enforcement would be difficult in any case. Dickert et al. (1981) developed a pilot program for Elkhorn Slough in Monterey County. Evaluation of that program and development of watershed management programs for other wetlands should be undertaken as soon as possible. In the meantime, we are faced with the disconcerting possibility that great leveed gashes across our wetlands may be their surest guarantee of a long future. This has so many drawbacks that alternatives which remove sediments on the landward side of coastal wetlands warrant serious consideration. The crucial question is whether they will perform properly when they have to.

7.3 OTHER WATER-BORNE CONTAMINANTS

Information on the water quality of the inlet streams and within Mugu Lagoon is limited. In a study of Revolon Slough (Figure 53a) from October 1980 to July 1981, mean concentrations of four pollutants were at or above hazardous levels for a marine environment according to EPA criteria: lead (approximately equal to the EPA standard), mercury (∿20x), silver (∿10x), and methoxychlor (∿20x) (Soil Conservation Service 1983). Revolon Slough is the tributary of Calleguas Creek that drains most of the intensively cultivated part of the Oxnard Plain. The flow of Calleguas Creek is ∿3x that of Revolon Slough. Since the former drains less-intensively cultivated land, the pollutants may be diluted before they enter the lagoon. The only determinations of water quality within the lagoon were confined to one location in the western arm (eight dates sampled, autumn 1974) and one in the eastern (two dates sampled, autumn 1974). Scans for 50 organic pesticides were negative, and elevated levels of heavy metals were not detected (Baker 1976).

Effluents from five sewage treatment plants discharging into Calleguas Creek provide significant sources of freshwater during non-rainfall periods. Apparently, the only times in recent years that sewage has been a problem followed breaks in sewer mains upstream. Ordinarily, effluents are treated to acceptable levels before discharge into the Calleguas Creek system. Nutrients from these sources are controlled by the State, whereas agricultural impacts are not controlled.

These data suggest that pollutants are a minor problem compared to inputs of sediments. However, the part of the lagoon most susceptible to the inputs (the central basin near the mouth of Calleguas Creek) has not been sampled. Also, spills upstream, such as breaks in sewer mains, could affect the lagoon. The absence of sport or commercial exploitation of the lagoon's living resources eliminates most of the human health hazards associated with pollutants; nevertheless, the potential for water-quality problems exists and has been insufficiently investigated.

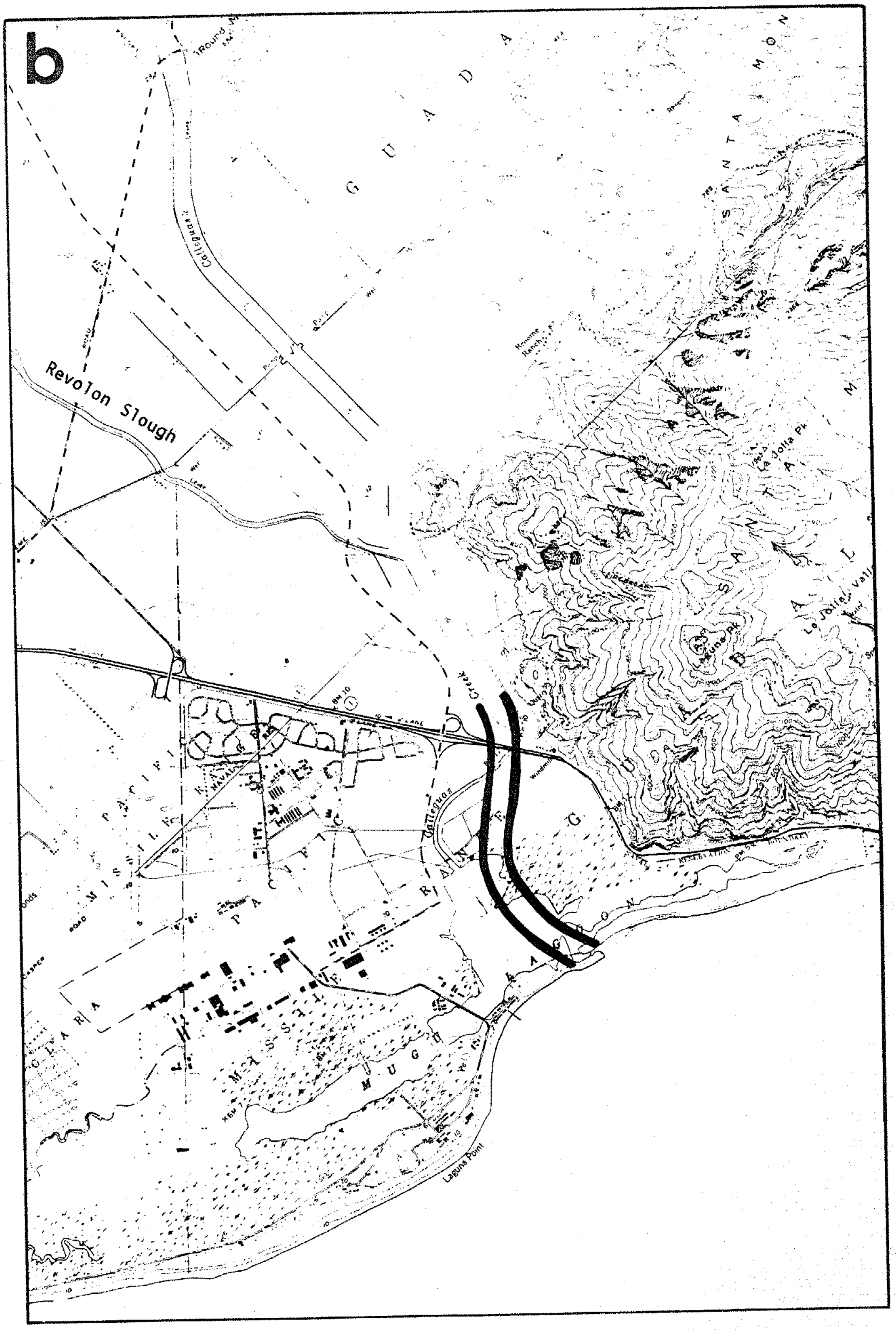
7.4 ALTERATION OF TIDAL FLUSHING

The estuarine ecosystems of southern California are differentiated first and foremost according to their extent of contact with the ocean. The permanently open, least modified wetlands are varied, usually densely populated ecosystems. Without doubt, tidal flushing is the most important property in determining the richness of the associated ecosystem. Tidal flushing is essential to the establishment of a broad spectrum of substrate types. Tidal flushing produces a wide variety of exposure-inundation regimes. Tidal flushing assures that some of the physicochemical stability of the marine environment is imparted to this protected, shallow water environment, thus bringing the wide variety of physical environments within the thermal, osmotic, and respiratory tolerances of many organisms excluded from enclosed wetlands in the southern California coastal region. Tidal flushing moves materials around, enabling organisms to exploit resources from areas from which the organisms are excluded, and removes wastes that might accumulate to harmful levels.

Because of the obvious benefits of tidal flushing and because of the stark contrasts between open and closed wetlands (or the same wetland when it is open as opposed to when it is closed), any alteration that reduces tidal flushing usually is assumed to degrade the affected wetland. Conversely, any alteration that augments tidal flushing usually is assumed to enhance the natural resources of the affected wetland, and such alterations commonly are proposed to restore degraded wetlands.

This was the logical basis for electing to open up the western arm of Mugu Lagoon to increased tidal flushing in compensation for the loss of wetland habitat to a military construction project. Indeed, the much earlier construction of a road had reduced the connection between the western arm and the central basin from 150 m wide to five 1.5 m x 1.5 m culverts. After the augmentation of the culverts by a 32-ft single-span bridge as specified in the restoration plan, the "normal diurnal tidal fluctuation" increased from 0.2 m to 0.7 m, and an

Figure 53. Two alternatives for channelization of Calleguas Creek proposed by the U.S. Army Corps of Engineers Los Angeles District in



1972. Revolon Slough is near the top. Heavy lines represent proposed channels (adapted from Macdonald 1976b).

additional 100 ha of salt marsh were flooded "during mean high tidal state" (Wolfe et al. 1979).

Little was known about the natural resources of the western arm prior to the augmentation of tidal flushing beginning in January 1979, and doubt remains as to what was enhanced and whether anything suffered. One federally listed endangered species, the salt marsh bird's beak (Cordylanthus maritimus), occurred prior to tidal alteration only in the western arm on the upper periphery of the marsh, and one species listed as endangered by the State of California, Belding's Savannah sparrow (Passerculus sandwichensis beldingi), was heavily concentrated in the upper part of the salt marsh surrounding the western arm. Both endangered species are still present and perhaps in greater numbers (R. Dow, pers. comm.).

The light-footed clapper rail (Rallus longirostris levipes) historically had been most abundant in the eastern and central parts of the lagoon and for several years had not been observed anywhere in the lagoon. The rail was again observed at Mugu Lagoon starting in 1983 and in increasing numbers since then. All recent sightings have been in the western arm (R. Dow, pers. comm.). Management considerations for endangered species are discussed further in Section 7.5. Unfortunately, observations on the more common organisms before tidal flushing in the western arm was augmented were inadequate to draw any conclusions about effects of the modification.

It is clear that we do not yet know enough about the function of the coastal wetland ecosystems of southern California to accurately predict the consequences of alterations. Therefore, we should approach restoration and enhancement activities with great circumspection and humility. Each project must be treated as an experiment at this early stage in the practice of coastal wetland restoration in southern California, with the most valuable product being better understanding to apply in future management rather than necessarily and unequivocally the enhancement of natural resources (Josselyn 1982; Zedler 1982, 1984). At the very least, the planning should include a systematic evaluation (list of educated guesses) of the responses of each category of natural resources (major functional groups of wetland organisms and endangered species), as well as the explicit identification of the expected prime beneficiaries of the alteration.

All future restoration projects must include inventories of natural resources before and after implementation, so that critical aspects of the performance of the project can be evaluated. Ideally, the pre-project inventory should be initiated soon enough to provide input for the final design of the project. Realizing that the commitment to project evaluation has to be commensurate with the size of the project itself, the option of performing a detailed evaluation of one or a few issues should be considered and perhaps encouraged in small projects, when a general assessment could only be perfunctory.

Finally, tests of specific ideas about wetland function that are highly relevant to restoration but are inadequately documented should be incorporated into restoration project designs. For example, the imputed limitation of salt marsh productivity by hypersalinity could be tested by purposely confining freshwater drainage to specific parts of an otherwise similarly configured restoration. Where possible outcomes are controversial, bet-hedging may be warranted. For instance, in a restoration plan for Los Cerritos wetland, brackish water impoundments were included for their presumed benefits to waterfowl, but because the concomitant increases in mosquitos might be unacceptable in adjacent residential areas, a failsafe was built in. The impoundment could be converted to a marine intertidal area by removing a single barrier (California State Coastal Conservancy 1982).

7.5 ENDANGERED SPECIES

Five endangered species occur in Mugu Lagoon. One species is a plant, the salt marsh bird's beak (Cordylanthus maritimus ssp. maritimus), and four species are birds: the light-footed clapper rail (Rallus longirostris levipes), Belding's

Savannah sparrow (Passerculus sandwichensis beldingi), California least tern (Sterna antillarum browni), and California brown pelican (Pelecanus occidentalis californicus). One brackish-water gastropod, Tryonia imitator, and two insects, the wandering skipper (Panoquina errans) and the globose dune beetle (Coelus globosus), have been or are now being considered for endangered status. In addition, the peregrine falcon, Falco peregrinus, is frequently sighted in the area (R. Dow, pers. comm.). The high concentration of endangered species in one location is the gravest testimonial to the limited extent and endangered status of the ecosystem. Clearly, the preservation and enhancement of these endangered species should be one of the highest priorities of management, next to the preservation and enhancement of the ecosystem itself. Unfortunately, efforts to preserve and enhance these populations are severely hampered by ignorance about their needs. This gap must be filled before programs for enhancement can be fruitful.

Two species are more tenuously connected with coastal wetlands than the other three and will be treated summarily. Pelicans mainly roost on a sand bar at the mouth of the lagoon. A few can be seen diving into the waters of the lagoon; however, they are a small minority of the pelicans present, suggesting that most of their feeding is offshore. In California, breeding is limited to colonies in the Channel Islands, most notably West Anacapa Island, 30 km west of Mugu Lagoon. The birds appear in the lagoon too early in the spring to come from the Channel Islands colonies, so it is likely that they come from colonies in the Sea of Cortez (U.S. Fish and Wildlife Service 1979). The relative immunity of this site from human disturbance is unusual in southern California, which may make it particularly valuable as a roosting area for pelicans. Because their use of the lagoon is limited primarily to roosting and no threat is foreseen for the area where they are concentrated, no management questions appear to be at issue.

Figure 54. California least tern (Sterna antillarum browni). (Photo supplied by U.S. Navy.)

The California least tern (Figure 54) is reported to feed primarily in estuarine waters but breeds colonially on beaches (U.S. Fish and Wildlife Service 1979). More recent observations indicate that adults feed mostly offshore, but that estuarine areas may be important for training the young to forage (Atwood and Minsky 1983). At Mugu Lagoon, least terns feed heavily in the tidal creeks of the western arm. The central arm, lower Calleguas Creek, and the settling ponds are used as areas for training the young. Least tern populations have varied erratically where observed and colonies have been abandoned for no apparent reason. The pattern, if it can be called that, is similar at Mugu Lagoon. In 1980 predation by red foxes appeared to be responsible for reproductive failure; however, nests have been abandoned in subsequent years when losses to predators were not evident (R. Dow, pers. comm.). At present, it would appear that observations at locations with more positive and consistent histories will have to provide the hints of how to proceed at Mugu Lagoon.

Salt marsh bird's beak (Figure 55) is a hemiparasitic annual plant (capable of completing its life cycle in the absence of host plants, but also capable of tapping into the vascular systems of other plants) that is limited to coastal locations between Carpinteria (Santa Barbara County, California) and Baja California. It is found mostly in patches in a narrow elevation range at the upper limit of tidal influence in salt marshes, where it is densest in or near open habitats. The occurrence at Mugu Lagoon is unusual in that many of the

Figure 55. Salt marsh bird's beak (Cordylanthus maritimus spp. maritimus). (Photo courtesy of U. S. Navy.)

colonies are separated from any tidal influence. Tests at Mugu Lagoon indicated that germination is completely suppressed at salinities exceeding 12 ppt, but increases after prolonged exposure of seeds to cold and is greater after 2 years of storage than when freshly collected (Murphey et al. 1981). Thus, the plant appears to be adapted to a highly variable soil salinity regime that excludes most other plants. Presumably, the suppression of germination except at low soil salinity and enhancement of germination after prolonged cold both increase the probability of completing development before salinities become too high for even the mature plants. Viability for at least 2 years provides for avoiding altogether growing seasons in which insufficient freshening occurs. The capability to parasitize other species may insure survival under conditions when salt marsh bird's beak would be competitively eliminated otherwise (abnormal persistence of low soil salinities, for instance).

Adaptation to a physical environment that eliminates most competitors and the hemiparasitic habit are not enough to insure a secure existence, however. The main reason for the plant's endangered status is human disturbance of its high-marsh habitat, either for real estate development or by trampling. The high marsh seems to be a favored habitat of the dune buggy and the dump truck, and the brittle salt marsh bird's beak is ill-suited to survive these invasions, even when transient. Its most serious natural enemies during observations at Mugu Lagoon were leaf roller larvae (Murphey et al. 1981). The depredations of this herbivore might be concentrated on salt marsh bird's beak, because other annuals of the high marsh habitat have very short life cycles, which may not allow the lepidopteran larvae to complete their life cycles.

Since 1978, the known populations of salt marsh bird's beak have been mapped each year, and since 1980 total cover, density, vigor, growth, and mortality have been monitored bimonthly on permanent transects, along with water depth and salinity and soil temperature, moisture, texture, and salinity (R. Dow, pers. comm.). Together with ongoing laboratory studies of propagation, these activities should provide an excellent and essential technical foundation for attempting to rehabilitate an endangered species, and this augurs well for the salt marsh bird's beak.

The primary habitat of the light-footed clapper rail (Figure 56) is the low marsh

Figure 56. Light-footed clapper rail (Rallus longirostris levipes). (USFWS photo.)

Spartina foliosa zone in four of the five locations where more than ten rails were counted during censuses in 1980 and 1981: Tijuana Estuary and Mission Bay Marsh in San Diego County, and Upper Newport Bay and Anaheim Bay in Orange County (Zembal and Massey 1981a, b). Zedler (1982) provides a recent summary of the status of the clapper rail in these areas, which justifiably emphasizes the crucial role of cordgrass for nesting and cover.

Sightings of rails in Mugu Lagoon have been few and far between. The virtual absence of cordgrass undoubtedly is part of the explanation, but another part is simply that systematic efforts to locate the birds were concentrated in the eastern arm where historically they had been most abundant (R. Dow, pers. comm.). Instead, the only sightings in recent years have been in the western arm. In spring 1983 a single rail was seen in the vicinity of a patch of freshwater marsh at the upper edge of the salt marsh, approximately 400 m from the tidal flats of the lagoon. In spring 1984, at least three pairs of rails were located (R. Zembal, U.S. Fish and Wildlife Service, Laguna Niguel, California; pers. comm.). All were seen near the western end of the western arm - on an isolated section of old berm in the middle of Salicornia marsh and along a tidal creek.

This information is meager; however, the association with freshwater marsh may be germane for future management. A statewide census of light-footed clapper rail populations in 1982 showed 22% of the State's population nesting in freshwater marsh or stands of freshwater reeds fringing salt marshes (Massey et al. 1984). In addition, at Upper Newport Bay, which supports three to four times the population of any other site and accounts for almost half of the State's population, freshwater marsh is used regularly by rails for foraging, roosting, and refuge during high tides and when alarm signals are given by other birds (Massey et al. 1984). These observations suggest that efforts at habitat enhancement for clapper rails in Mugu Lagoon should include the expansion and protection of patches of freshwater marsh within the salt marsh and fringing its upland edge, since the rail's preferred habitat of tall, dense Spartina is so rare.

The other direction to look for guidance in promoting the rail population of Mugu Lagoon is toward Carpinteria Slough in Santa Barbara County, the fifth of the sites that supported more than ten pairs of rails in 1980 and 1981. Spartina does not grow in Carpinteria Slough now and probably did not historically (W. Ferren, University of California, Santa Barbara; pers. comm.). The attributes of this marsh that provide such good habitat for rails in the absence of Spartina have not been analyzed but should be. This most northerly site in the current distribution of the rails probably would serve as a more valuable model for management at Mugu Lagoon than the more southerly sites where Spartina is so important. Patches of freshwater marsh interdigitate with the upland edge of the salt marsh at Carpinteria Slough, and rails are in the patches or on their edges (pers. observ.). Also Carpinteria Slough has a well-developed system of tidal creeks, in common with other sites where rails are relatively abundant (Zembal and Massey 1983). More detailed comparisons should be made.

The Belding's Savannah sparrow (Figure 57) appears not to be in so perilous a state as the clapper rail, presumably because its preferred habitat is much more widespread than the rail's. The sparrow is found mainly in the middle and upper parts of the salt marshes, especially where pickleweed (Salicornia

Figure 57. Belding's Savannah sparrow (Passerculus sandwichensis beldingi). (Photo courtesy of U.S. Navy.)

virginica) predominates. It eats insects, Atriplex seeds, and Salicornia tips (Massey 1979). California king snakes have been observed to be a significant predator on sparrow eggs in the eastern arm of the lagoon (S. Davis, Pepperdine University, Malibu, California; pers. comm.). Massey (1979) provided an excellent account on most aspects of its biology.

Mugu Lagoon supports one of the two biggest surviving populations of the Belding's Savannah sparrow, consistent with the large expanses of Salicornia marsh surrounding the lagoon. The contrast between the high density of sparrows in the western arm and the low density in the eastern arm is the feature of greatest interest for management. The value of this contrast for management lies in the contradiction between the commonly perceived "degraded" status of the western arm (for instance, U.S. Fish and Wildlife Service 1979) and the obvious much higher carrying capacity of the western arm than the eastern arm for this endangered species. It remains to be determined why occurrence of the Belding's Savannah sparrow violates perceptions of degraded wetland at Mugu Lagoon and elsewhere (Massey 1979).

Endangered species pose some serious dilemmas. The serious straits that they are in seem to demand that we take immediate action, yet we may understand their needs so imperfectly that our actions could well prove to be detrimental. Our ignorance argues for intensive study, yet intensive study may necessitate disturbance that causes unacceptable harm to an already beleaguered species. Even when an alteration is clearly beneficial for one endangered species, it may be detrimental for another endangered species. Since so many endangered species are concentrated into the fragments of coastal wetlands remaining in southern California, these conflicts are likely to be frequent and serious. Therefore, when alterations are made, they should be conducted as experiments, and their outcomes should be closely scrutinized before the same kind of alteration is implemented again.

7.6 INFORMATION GAPS

Mugu Lagoon probably has been studied more intensively than any other estuary in southern California. However, information gaps remain, as noted throughout this profile. The most important gaps are the lack of information about nutrients and the paucity of information about the western arm, except for birds. The lack of information about nutrients necessitated a speculative analysis of the influence of nutrients on the structure and function of the rest of the ecosystem, which relied on inferences drawn from the physical characteristics of the system and the characteristics of primary producers in different parts of the system. The analysis led to a series of hypotheses suggesting that ample tidal flushing might be responsible for low salt marsh productivity in the eastern arm of Mugu Lagoon. This interpretation is consistent with available information as far as that information goes, but is at odds with the findings in most other systems. Therefore, the whole topic of nutrient supply, availability, and use must be studied before we can understand functioning at the base of the ecosystem. The analysis in this profile should be treated as a set of hypotheses, provocative but as yet untested.

The paucity of knowledge about the western arm of the lagoon is a critical concern for the future management of the estuary for a number of reasons: (1) The western arm and the central basin are the parts of the lagoon that have been most impacted by past human alterations. Therefore, remedial actions should be focused in these parts. (2) The ongoing operations of the naval base around the western arm will necessitate other alterations in this part of the lagoon in the future. (3) If the Soil Conservation Service's (1983) predictions about sedimentation in the rest of the estuary hold true, the western arm will be the only part of the lagoon where estuarine habitats will persist. (4) The activities of four of the five endangered species resident in or using Mugu Lagoon are concentrated in the western arm (salt marsh bird's beak, Belding's Savannah sparrow, light-footed clapper rail, and California least tern). Since the needs of present and future management will be concentrated in the western arm of the lagoon, yet little of what we now know applies with certainty to this part of the ecosystem, a high priority of management should be the support and encouragement of ecological research in the western arm. Although any information about the biota and the environmental regime of the area would be valuable, the needs of the endangered species certainly should be studied, including comparisons with other systems that might serve as models for designing habitat improvements. Currently, the Navy is supporting valuable research on endangered species in the western arm. Trade-offs for different segments of the biota should be evaluated for increasing tidal exchange. Increased tidal exchange may mean more complete drainage of areas which could be detrimental for organisms dependent on surface water. This applies to areas that are seasonally flooded because of road berms or dikes, as well as areas where tidal exchange is only restricted.

Although considerable information has been gathered on the use of the lagoon by fishes, three aspects of fish biology require more attention.

(1) Use of tidal creeks. No information is available for Mugu Lagoon. Studies in Elkhorn Slough (Barry and Cailliet 1981) and Tijuana Estuary (Nordby 1982) indicated heavy use by juveniles and especially larvae of some species. Thus, retention of some water in tidal creeks should be insured when alterations to increase tidal exchange might result in drainage to lower elevations, as has occurred in the western arm.

(2) Halibut nursery. The possible dependence of California halibut, prized by sport and commercial fishermen alike, on estuarine areas as nursery grounds (Plummer et al. 1983) and the abundance of halibut in the eastern arm of Mugu Lagoon (Chapter 4; Onuf and Quammen 1983) suggest that better information about habitat requirements and distribution in the rest of the lagoon is desirable.

(3) Shovelnose guitarfish nursery. The southern California fishery for sharks and other elasmobranchs has expanded greatly in recent years and now includes the taking of shovelnose guitarfish (M. Love, Occidental College, Los Angeles, California; pers. comm.). The concentration in Mugu Lagoon of very large females, carrying large eggs and embryos (Chapter 5; DuBois 1981), indicates that Mugu Lagoon and other southern California estuarine systems usually open to the sea might be important to the stock. Therefore, the unusual characteristics of the shovelnose guitarfish's use of the lagoon merit more study.

This list of information gaps is indicative rather than exhaustive. The most important function that this profile can serve is to provide the framework for efficiently filling those gaps and others that become evident later.

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16. Abstract (Limit: 200 words)

Mugu Lagoon is significant as one of the least disturbed and best protected estuaries in southern California; thus, this small estuarine system can serve as a baseline model for the region. This report summarizes and synthesizes scientific data on the ecological structure and functioning of the estuary, including discussions of climate, hydrology, geology, physiography, biotic assemblages, and ecological processes and interactions.

The estuary exhibits extreme variability in freshwater inputs, being at times totally marine and at other times flushed by stormwater runoff from the watershed. Major storms in 1978 and 1980 resulted in sedimentation that drastically altered benthic communities and resulted in changes in the distribution of submerged aquatic vegetation and benthos, and fish and shorebird use of these food resources.

Mugu Lagoon is part of a naval base and therefore not subject to the development pressures facing many other southern California estuaries. Storm-produced sedimentation remains a management concern, as well as closure of the mouth of the lagoon due to littoral drift of sand along the barrier spit.

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