

**ILTER: Land/Ocean Interactions and the Dynamics of Kelp Forest  
Ecosystems**

PI/PD DEPARTMENT

Marine Science Institute  
University of California  
Santa Barbara, CA 93106,  
United States

PI NAME      Telephone Number      Electronic Mail Address

Daniel C Reed      805-893-8363      [reed@lifesci.ucsb.edu](mailto:reed@lifesci.ucsb.edu)

Co-PI

Scott D Cooper      805-893-4508      [scooper@lifesci.ucsb.edu](mailto:scooper@lifesci.ucsb.edu)

Co-PI

Steven D Gaines      805-893-7379      [gaines@lifesci.ucsb.edu](mailto:gaines@lifesci.ucsb.edu)

Co-PI

Sally J Holbrook      805-893-3956      [holbrook@lifesci.ucsb.edu](mailto:holbrook@lifesci.ucsb.edu)

Co-PI

John M Melack      805-893-3879      [melack@lifesci.ucsb.edu](mailto:melack@lifesci.ucsb.edu)

## PROJECT SUMMARY

---

The project summary should include a statement of objectives, methods to be employed, and the significance of the proposed activity to the advancement of knowledge or education. Avoid use of first person to complete this summary. **DO NOT EXCEED ONE PAGE.** (Some Programs may impose more stringent limits.)

An LTER (Long-Term Ecological Research) site is proposed for the Santa Barbara region that will focus on ecological systems at the land/ocean-margin. This location is typical of many semi-arid regions in that it includes a large number of watersheds with episodic stream flow that vary in size and land use. The focal coastal ecosystem of our proposed research will be giant kelp (*Macrocystis pyrifera*) forests, which are extremely important to the ecology and economy of coastal areas along the west coast of North and South America. Kelp forests occur on shallow coastal reefs and are affected in both positive and negative ways by land and the open ocean through the movement of water carrying constituents (e.g. sediments, nutrients, larvae, pollutants) from these different sources. Kelp forests have a unique trophic structure in which producers (macroalgae) and consumers (sessile invertebrates that filter plankton) compete for space. Competition between macroalgae and sessile invertebrates can be mediated by the relative supply of nutrients and particulate organic matter to the reef.

Although several lines of evidence suggest that the effects of terrestrial runoff on kelp forests in the Santa Barbara Channel can be large, the relative contributions of land vs. ocean derived constituents in structuring this and other coastal ecosystems in the region is poorly understood. Interdisciplinary research coordinated among 22 investigators is proposed that will examine questions and hypotheses related to all five core areas of research shared by LTER sites. The key issues that will specifically be addressed are (1) spatial and temporal scales over which terrestrial runoff and ocean forcing perturbs kelp forest ecosystems, (2) patterns and processing of organic matter in the ecosystem, (3) patterns of organic and inorganic inputs and their movement from the land to the coastal zone, (4) the effects of terrestrial runoff on patterns and controls of primary production in kelp forests, and (5) the effects of terrestrial runoff on the long-term population dynamics of key kelp-forest species and on trophic interactions. Regional studies will combine satellite imagery and field measurements of discharge from 3 primary and 12 secondary watersheds with modeling of solute and sediment-discharge relationships to determine patterns of runoff entering the Santa Barbara Channel. Detailed sampling of water chemistry and short and long-term experiments will be done in the three primary watersheds to determine smaller scale processes that are critical in controlling overall export to coastal waters. Satellite imagery combined with detailed measurements of ocean currents, waves, suspended sediment, subsurface irradiance, and seawater chemistry collected from moored instruments in the kelp beds offshore of the three primary catchments will be used to determine the timing, spatial extent, and residence time of runoff in the coastal zone and the degree to which they are modified by ocean processes.

The effects of runoff on patterns of primary production will be investigated for both phytoplankton and macroalgae (the two major groups of primary producers found in kelp forests). Phytoplankton production will be estimated from optical data collected from moored instruments and satellites, chlorophyll concentration data collected from moored instruments and ocean cruises and  $C^{14}$  uptake experiments. Kelp production will be estimated from in situ measurements of growth and survival of tagged individuals and aerial photos of surface canopy area. Experiments will be done to evaluate factors that control primary production and the degree to which they are influenced by land and ocean processes. Short and long-term experiments and modeling will be done to determine the extent to which changes in nutrient supply due to runoff alter trophic interactions of the unique food web.

## ***Section 1 -- Results from Prior NSF Support***

\*publications for each award are listed by their reference number in *Section 3 - References*

Mark Brzezinski

Award: OCE-9401990, Amount: \$270,000, Period of support: 10/1/94 – 10/1/98, Title: Silica cycling and the role of *Rhizosolenia* mats in elemental cycling in the central North Pacific  
Summary: Cruises were conducted from Hawaii west along ca. 27°N in August 1995 and from Hawaii east along 31°N in July 1996. This was the first study of silica cycling in an oligotrophic mid-ocean gyre other than the Sargasso Sea. We discovered that average silica production rates in the Central North Pacific (CNP) are nearly three times higher than in the Sargasso Sea suggesting that mid-ocean gyres contribute significantly more to global silica production than previously thought. We examined the hypothesis that silica production by *Rhizosolenia* mats was significant to the regional silica cycle. We combined direct measurements of silica production rates by mats collected using SCUBA with surveys of mat abundance to 150 m using a remote video system by to estimate integrated silica production by mats. The result was that silica production by *Rhizosolenia* mats in the CNP was nearly equal to that of the entire diatom assemblage of the Sargasso Sea. Including mats in the regional silica budget for the CNP increases the average silica production rate for the region by 26% to 1.5 mmol Si m<sup>-2</sup> d<sup>-1</sup>. The camera system revealed that mat abundance was >10 fold higher than previously estimated by divers due to the ability of the video system to image small mats. Those new data showed that the vertical transport of nitrate by migrating mats was a significant source of new production in the CNP exceeding that resulting from vertical eddy diffusion.  
Publications: Ref # 18, 258, 259, 282

Scott Cooper

Award: DEB-9407591, Amount: \$300,000, Period of support: Aug. 1, 1994-Aug. 31, 1998, Title: Effects of consumers on spatial heterogeneity in their resources in streams.  
Summary: NSF Grant DEB-9407591 has funded research on the effects of consumers and nutrients on the densities and spatial heterogeneity of organisms in streams. Since the start of this grant in summer, 1994, my colleagues, graduate students, postdoctoral associates, undergraduate assistants, and I have conducted field experiments, and laboratory and computer analyses, dealing with the effects of consumers and resources on stream organisms. Our work has focused on five research areas: (1) the development of population models of open (stream) systems including behaviorally flexible organisms; (2) the experimental evaluation of the effects of top carnivores (trout, stoneflies) on mean levels, variability and spatial heterogeneity of resources (benthic invertebrates and algae) at lower trophic levels (conducted in large, artificial stream channels and in even larger, natural stream sections at the Sierra Nevada Aquatic Research Laboratory, SNARL, near Mammoth); (3) analysis of the effects and responses of stream grazers to algal patchiness; (4) the experimental evaluation of factors affecting predator-prey interactions in streams, including prey refuges, prey resource levels and distributions, and prey migration rates; and (5) experimental work on the effects of nutrient enrichment gradients on algae and grazing insects.  
Publications: Ref # 27, 28, 47, 60, 129, 143, 144, 194, 195, 203, 227

Thomas Dunne

Award: EAR-9628737, Amount: \$96,196, Period of support: 09/01/96 – 08/31/98, Title: *Distribution and Evolution of Geomorphic Process Zones in Large Mountain Ranges*  
Summary: To demonstrate that systematic variations in erosion rate of the Eastern Cordillera of the Bolivian Andes result from unsteady tectonic uplift, we collected rock samples for apatite fission track analysis (AFTA) to define spatial patterns of long-term average denudation rate. We documented systematic variations in such rates in three headwater transects in the Cordillera, oriented across the axis of uplift variation. We then developed a simple power-based model of channel incision, calibrated it against tephra geochronology on rock straths in the region, and calculated the regional channel network incision history for the range. The measured spatial

variations in denudation rate are consistent with a transient response by the channel network to unsteady, non-uniform uplift. In order to refine interpretations of AFTA, we modeled the influence of realistic two-dimensional topography on cooling ages of apatite crystals in rock that is being exhumed at rates typical for active orogens. We also analyzed Guyot's (1993) compilation of water and sediment discharge at 55 gauging stations in the Bolivian Andes to understand controls on erosion rates in mountain basins and thus the source strength of the Andean sediment supply to the foreland basin. The results show a strong dependence of mountain sediment yield on mean basin slope and lithology, but only a weak effect of precipitation or vegetation cover. Extrapolating the resulting sediment yield equation to the rest of the Amazonian Andes, we are able to make a first-order estimate of the yield of sediment to the Amazon River.

Publications: Ref # 231, 232, 274

Steven Gaines.

Award: OCE-9402690. Amount: \$408,796; Period of support: 6/15/94 to 5/31/98; Title: Is variable retention of larvae nearshore a general cause of variable recruitment?

Summary: Our prior work on settlement of barnacles in New England suggested that among year and among site variation was largely due to variation in retention of larvae nearshore. When larvae were retained nearshore, recruitment rates were substantially higher than when larvae were transported far from shore. The primary source of variation in nearshore retention was variation in terrestrial runoff into bays. Large flows from terrestrial watersheds increased the transport of larvae away from shore. This study evaluated whether this source of larval variation applied to other species and the consequences to community interactions. Many species showed positive covariance in settlement because of shared sources of variable recruitment. Species interactions and community structure were strongly affected by this covariation among species. Some of the interspecific interactions were positive for both species, others were negative for at least one member of the pair. As a consequence, positive covariation in settlement had strikingly different effects on community structure. By increasing the intensity of the interaction, shared sources of recruitment variation could either enhance population sizes or reduce them.

Publications: Ref # 7, 8, 41, 75, 76, 77, 92, 146, 147, 148, 275, 292

Sally Holbrook

Award: OCE91-02191, Amount: \$260,955 Period of support: 9/91-8/94, Title: Population Regulation in a Temperate Reef Fish System

Summary: Our long-term studies of 2 species of surfperch, reef fish that annually produce a small number of non-dispersing young, have revealed the following. (1) Competition between the species had a substantial adverse effect on mean density, but explained little of the variation in adult abundance among 11 reefs, and almost none of the dynamics over 9 years. (2) Variation in adult densities in space and time was well explained by spatial and temporal variation of food-related resources (i.e., species-specific foraging habitat). (3) Fluctuations in adult densities ranged from quite small to large among reefs; local fish dynamics reflected local resource dynamics. Local dynamics of the 2 surfperches were not correlated within a site as critical resources fluctuated independently. For either species, patterns of dynamics were less similar for populations > ~1km apart, suggesting that events influencing dynamics were extremely localized. (4) Populations of both species tracked fluctuations in their respective resource, primarily through demographic responses. (5) Per capita production of young varied with food available per female, obscuring relationships between numbers of adult and young produced. The number of young produced in a year was well predicted by the amount of food resource at a site. (6) Survivorship of newborns to age 1 generally was high, and only declined when food resources declined sharply after birth. In sum, local populations of both surfperches appeared regulated by localized, density-dependent processes that mostly affected local production of (non-dispersing) young, and fluctuations in abundance reflected local resource dynamics.

Publications: Ref # 50, 103, 109, 110, 111, 113, 115, 117, 119, 204, 244, 266

Patricia Holden

Award: DEB-9805946, Amount: \$74,897, Period of support: 9/01/98-2/28/00, Title: Microscale mechanisms in unsaturated biofilm substrate availability: a molecular reporter system approach.

Summary: This project was awarded in September 1998. Thus far, we have genetic constructs of *Pseudomonas aeruginosa* PG201 that have been engineered to express the gene for GFP when the genes encoding for the production of a bioemulsifying protein are transcribed. We are currently testing the engineered strain to determine its responsiveness to a range of substrates. We are using denaturing gradient gel electrophoresis general mutational analysis and community analysis of aquatic samples for determining the origins of pathogens in aquatic environments.

Publications: none to date

John Melack

Award: DEB95-08733, Amount: \$250,000, Period of support: 06/95-06/00, Title: Responses of a saline lake to environmental change from seasonal to decadal time scales.

Summary: Large amounts of snowmelt runoff in 1995 led to the onset of persistent chemical stratification (meromixis) in Mono Lake, and a major portion of our research during this grant has focused on meromixis and its ecological effects. We hypothesized that the reduction in vertical mixing caused by meromixis would reduce nutrient supply and decrease primary productivity by phytoplankton and secondary productivity of invertebrates (*Artemia monica*) and birds. Furthermore, our application of a mechanistic model of vertical mixing indicated that meromixis is likely to persist for several decades (127, 128, 228, 229). To better understand mixing processes, we conducted physical microstructure profiling in concert with deployment of thermistor chains and measurement of nutrient and phytoplankton profiles. These efforts indicated that most of the vertical fluxes of heat and nutrients occurred near shore due to boundary mixing initiated by high wind events (151, 152). An analysis of the major differences between monomictic (mixing once per year) and meromictic periods (161) revealed that both primary productivity and *Artemia* biomass declined under meromixis. Nearly all aspects of the life-history of *Artemia* were affected by reduced food levels accompanying the onset of meromixis. Collaborative efforts are underway to assess the impacts of meromixis and changes in the annual zooplankton dynamics on the breeding gull colony and migrating grebe populations. In addition, we have analyzed sediment cores to determine organic matter accumulation during the past 170 years (126) and to assess spatial variability in deposition rates.

Publications: 126, 127, 128, 151, 152, 161, 228, 229

Roger Nisbet

Award: DEB-9319301, Amount: \$271,000, Period of support: 03/94-02/98, Title: Models relating population dynamics to individual physiology and behavior.

Summary: This grant supported research on individual-based population models as a component of testable, ecological theory. *Daphnia* was chosen for this work because: (1) it is important in many natural ponds and lakes and any understanding gained from modeling its population is likely to be ecologically important and capable of generalization; and (2) because the physiology and environmental responses of individuals (and populations) of the commoner *Daphnia* species is well documented, this system affords the possibility of studying the individual-to-population link in systems of increasing complexity. Our main achievements were: (1) Increased insight into the population dynamics; in particular knowledge of which attributes of individuals play a significant role in stabilizing real populations; (2) Sharper understanding of the processes of formulating, testing, and simplifying individual-based models; and (3) New general theory.

Publications: Ref # 39, 48, 89, 90, 91, 149, 156, 173, 174, 176, 178, 179, 180, 181, 182, 183, 185, 288

Daniel Reed

Award: OCE92-01682; Amount: \$288,234; Period of support: 8/1/92 - 7/31/96, Title: Variation in propagule supply and its role in kelp-forest regeneration

Summary: During this award we measured reproductive responses of the giant kelp, *Macrocystis pyrifera*, (a species that reproduces continuously) during a 3 year period in which resources and environmental conditions fluctuated greatly and contrasted these responses to those of the palm kelp, *Pterygophora californica*, a sympatric species that exhibits strictly seasonal reproduction. We found that the quantity and quality of spore production tracked nutrient levels within and among years for *Macrocystis*, but not for *Pterygophora*. These findings support our general hypothesis that environmental conditions and resource availability exert a much greater influence on the quantity and quality of offspring production in species that reproduce continuously than on the majority of species that are strictly seasonal in onset of reproduction. We found that the propagules of these kelps have little capacity for dormancy and the vast majority of kelp plants originate from newly settled spores. We found that patterns of spore release in both *Macrocystis* and *Pterygophora* differed significantly from that expected under asynchronous conditions. Greatest pulses in spore release coincided with large storms which were also found to promote dispersal and early survival of recently settled spores. Thus, while storms are an important source of disturbance to kelp, they also play a critical role in ensuring their rapid recovery.

Publications: Ref # 17, 29, 30, 212, 218, 219, 220, 223

O. J. Reichman,

Award: DEB-94-21535, Amount: \$2,000,000, Period of support: 5/1/95 – 4/30/00, Title: National Center for Ecological Analysis and Synthesis.

Summary: NCEAS (<http://www.nceas.ucsb.edu>) provides the opportunity and facilities for intense collaborative research on major fundamental and applied problems in ecology. Since May 1995 the Center has hosted over 1400 visiting scientists and sponsored 25 workshops, 24 working groups, 22 visiting scientists and sabbatical fellows, and 16 postdoctoral fellows. NCEAS' mission includes leadership in the development of new methods appropriate to advancing synthetic and integrative work in the ecological sciences. Through experience with our research groups, the scientific computing staff at NCEAS have identified a critical need for better tools and standards for the integration and preservation of disparate ecological data, and have become involved in a number of informatics initiatives to address these issues

Publications: > 200 (not listed in Section 3 References).

Josh Schimel:

Award: DEB-9211769; Amount: \$330,000, Period of support: 1992-2000, Title: Successional Processes in Taiga Forests: Bonanza Creek LTER.

Summary: My research at Bonanza Creek covered several general areas: 1) C and N cycling in taiga ecosystems, 2) controls on CH<sub>4</sub> consumption, and 3) the role of microbial community structure in ecosystem processes. Process studies and measurements on C cycling focussed on environmental controls on CO<sub>2</sub> production and flux across taiga succession. Work on N cycling examined the effects of plant secondary chemicals on N cycling in alder and poplar soils. While simple phenolics and low molecular weight tannins may act as microbial substrates, heavier weight tannin fractions act as microbial inhibitors, and different microbial communities show different levels of adaptation to chemicals. Work on CH<sub>4</sub> consumption focussed on understanding the role of different microbial communities in controlling CH<sub>4</sub> consumption. Finally in the area of microbial community structure, I focused on linking microbial and ecosystem scales of life, identifying the types of processes that are sensitive to microbial community composition. I showed that 'broad processes' (physiologies widely distributed across taxa, or which are the sum of many individual processes, such as SOM breakdown) are insensitive to differences in community composition. However, 'narrow processes' (specific physiologies carried out by a limited group of organisms) can be sensitive to differences in community composition, even at the ecosystem scale.

Publications: Ref # 20, 21, 22, 33, 84, 85, 86, 87, 88, 234, 235, 236, 237, 238, 239, 240, 273, 240, 273, 284, 285,

Russell Schmitt

Award: OCE9503305, Amount: \$650,035, Period of support: 7/1/95-6/30/00, Title: On the Abundance and Dynamics of Damselfish in the Genus *Dascyllus*

Summary: The objectives of this study were to examine local processes that affect abundance and contribute to population regulation of reef fish, and to develop a protocol to quantify the effects of simultaneously-operating processes on local population dynamics. Our work revealed 2 sources of density-dependent interactions that bound fluctuations in local abundance of several species of damselfish in the genus *Dascyllus*. The first involves interactions between potential larval settlers and residents on a microhabitat. Compared with unoccupied microhabitats, settlement rates were enhanced at low but depressed at high densities of resident conspecifics. This produced a strong local regulatory mechanism by lowering the probability of local extinction when habitats were greatly under-saturated, and slowed net growth rates as habitats approached saturation. The second source of local regulation is density-dependent mortality, which was strongest for the initial few days after settlement due to predation. In multi-year-long colonization transplantation experiments we found that spatial variation in abundance was influenced by both larval supply and availability of suitable microhabitats. Densities reached on all transplanted microhabitats were sufficient to suppress subsequent settlement by 80-90%, indicating that habitat became limited. At average supply rates density-dependent limitation was twice as great as supply limitation, and both exceeded density-independent limitation. How far the local system is from saturation determines which process predominates.

Publications: Ref # 111, 112, 113, 114, 118, 243, 251, 252, 253, 254, 255, 267, 268, 288

David Siegel

Award: OCE-9525826, Amount: \$340,000, Period of support: 11/95- 10-00, Title: Quantification and Parameterization of Solar Radiation Penetration and Heating in the Pacific Warm Pool

Summary: The links between solar radiation penetration, near-surface radiant heating, and the thermal structure of the western Pacific warm pool mixed layer are being investigated using in-situ data and models. Several new aspects of solar radiation penetration and heating for the range of atmospheric and oceanic conditions found in the western Pacific warm pool during TOGA COARE (Tropical Ocean Global Atmosphere, Coupled Ocean Atmosphere Response Experiment) will be evaluated in order to model the processes by which solar radiation regulated the sea surface temperature and the mixed layer heat content of the warm pool.

Publications: Ref # 188, 189, 190, 191, 207, 259

Libe Wasburn

Award: OCE96-33329, Amount: \$380,000, Period of support: 01/01/97 – 12/31/00,

Title: Variability in kelp spore dispersal and its role in kelp population dynamics

Summary: The objectives of our research are to predict the frequency of occurrence and relative importance of the physical and biological conditions that promote extended spore dispersal in giant kelp (*Macrocystis pyrifera*) and to determine the role of spore immigration rates in regulating the dynamics of local kelp populations. We are collecting time series describing local water movement simultaneously with measurements of spore release and dispersal from isolated plants over a wide range of physical and biological conditions. To characterize the near-bottom flow, we are measuring currents throughout the water column along with turbulent velocities at the spore release depth. We are using this information to build an individual-based model that will predict effective spore dispersal within and away from a local population for varying conditions of water motion, plant fecundity, plant spacing, spore release, and population size. Predictions from the model will be tested using an experimental population of adult plants. The general significance of this work is that it will provide much needed insight into the hydrodynamic conditions, such as wave height, bottom turbulence levels, and flow speed that promote extended propagule dispersal, and the degree to which propagule immigration influences the dynamics of species perceived to have relatively closed populations.

Publications: 220, 221, 222

## ***Section 2 -- Main Proposal***

### **INTRODUCTION**

Most studies of land/ocean interactions have been done in areas with wet regional climates and large watersheds (e.g., Chesapeake Bay, Columbia River, Plum Island Sound, & the coast of Georgia). In contrast, many regions, particularly western continental margins at middle latitudes (20° to 40° N and S), are relatively arid or have strongly seasonal patterns of rainfall. Terrestrial input from these watersheds into the coastal zone tends to be episodic and may occur only during a portion of the year. The reduced rainfall greatly influences the plant community and alters the role of fire and grazing as sources of disturbance. Coastal ecosystems in semi-arid regions are likely strongly influenced by terrestrially-derived input, albeit in ways that are quite distinct from the effects seen in regions with larger watersheds with continuous riverine flows.

In addition to a limited geographical/climatological focus, existing studies of land/ocean interactions have had a specific habitat focus. The focal ecosystem in most studies of land/ocean interactions has been the estuary at the mouth of the watershed, even though terrestrial impacts on coastal communities extend well beyond these interface habitats. Runoff and its constituents leave the estuary and enter the coastal ocean. The terrestrially-influenced coastal zone includes a variety of marine habitats outside the estuary, such as rocky reefs, where responses to runoff may differ from those in estuaries because of:

- *Different suites and scales of processes* -- The nature of land/ocean interactions on coastal reefs is qualitatively different from those in estuaries. In particular, terrestrial influences will interact with a much broader range of ocean processes outside the estuary. In coastal reefs there are ocean influences of waves, longshore currents, and basin-wide patterns of circulation. The scales of variation in these ocean processes are large, and the nature of their interactions with terrestrial inputs from watersheds is poorly understood.
- *Different terrestrial inputs because estuaries act as filters* -- From the standpoint of coastal reef ecosystems, wetlands and estuaries at the mouth of watersheds may play important roles as “filters” that alter the composition and quantity of materials entering the ocean (Nixon 1980, Jordan et al. 1991). The quantity and quality of sediments, nutrients, and pollutants can all differ upstream versus downstream of the estuary. Therefore, coastal reefs will experience different terrestrial inputs from those reaching the estuarine wetlands.
- *Different taxonomic groups* -- The dominant taxa in estuarine communities can differ substantially from those in coastal reef communities. For example, vascular plants such as eelgrass or marsh grass are typically the dominant primary producers in estuarine wetlands, whereas macroalgae dominate coastal reefs. The species diversity of macroalgal dominated systems is typically higher throughout the food web.
- *Different food web structure* -- The food web and interaction webs of coastal communities are quite different outside versus inside of estuaries. The primary distinction is the common occurrence of strong competition *across* trophic levels through interactions between attached primary producers (macroalgae) and sessile invertebrate suspension feeders. These two potentially competing space occupiers represent two competing pathways for primary production to enter the community -- one based on local primary production by macroalgae, the other based on more regional primary production by phytoplankton.

This suite of differences suggests that the terrestrial influences on coastal reef communities may be dramatically different from their effects on estuarine communities even when they are influenced by the same watersheds. We explore these likely differences in greater detail below.

### **LAND-OCEAN INTERACTION IN A SEMI-ARID REGION**

Here, we propose a new land/ocean LTER site in the Santa Barbara region, along the coast of southern California. This location is typical of many semi-arid regions in that it includes a large number of watersheds with episodic stream flow that vary in size and land use. The focal marine ecosystem of our proposed research will be giant kelp (*Macrocystis pyrifera*) forests, which are extremely important to the ecology and economy of coastal areas along the west coast of North and South America (Foster and Schiel 1985, Leets et al. 1992). Giant kelp forests are among the

most productive communities in the world, comparable for example to tropical rain forests (Mann 1973, Foster and Schiel 1985). Similar comparisons with tropical forests have been made with regards to the high species diversity of giant kelp forests (Darwin 1860). The complex food web of the kelp forest includes a diverse array of primary producers (of which the most important species is *M. pyrifera*), primary, secondary and tertiary consumers, and decomposers. Although kelp is the primary food for a diverse array of species (Foster and Schiel 1985), most kelp biomass is not consumed directly (Gerard 1976, Harrold and Pearse 1987), but instead enters the food web indirectly as particulate or dissolved organic matter. Kelp derived carbon provides a significant food source for a diverse assemblage of nearshore suspension feeders and is found in abundant quantities throughout the coastal food web (Duggins et al. 1989).

Despite the episodic nature of stream flows from watersheds in semi-arid regions, terrestrial influences on kelp forests may be large. To identify the coupling of land/ocean processes, we start by compartmentalizing the system into four components (1) upland watershed, (2) estuarine "filter", (3) terrestrially-influenced coastal zone (TICZ), and (4) open sea (Fig 1).

Kelp forests occur within the TICZ and are affected by land and the open ocean through the movement of fluids carrying constituents derived from these different sources. The major constituents affecting kelp forests can be classified into four groups: 1) Sediments, 2) Nutrients and organic matter, 3) Individuals (e.g., spores & larvae), and 4) Pollutants. Some of these constituents have direct positive effects on population sizes of kelp forest species (e.g., larvae), and others may reduce population sizes by acting as a disturbance (e.g., sediments). Some components may enhance individual performance (e.g., nutrients, plankton and terrestrially derived organic matter for food), while others reduce it (e.g., pollutants). The relative contributions of these constituents from land versus ocean sources is largely unknown, but several lines of evidence suggest that terrestrially derived influences can be large.

First, consider the input of sediments. Sediments are an important source of disturbance for shallow reef communities because they bury rocky substrata occupied by algae and invertebrates and reduce light penetration for primary production. Satellite imagery now allows us to estimate sediment concentrations in surface waters. Figure 2 shows an image of the Santa Barbara Channel from early 1997, during the period of peak flows for the year. The sediment plumes emanating from different watersheds in the region are clearly visible in the image. The scale of sediment influence varies substantially from one watershed to the next. Around large rivers, the level of sediment disturbance is so large that rocky reefs do not occur within 10 km of their mouths (Ambrose et al. 1989).

Other sections of the coastline show little sediment input from terrestrial watersheds. Similar images from other years or seasons suggest that temporal variation in terrestrially derived sediment input is also quite large. These patterns suggest that the disturbance regime associated with watershed runoff will be highly variable in space and time.

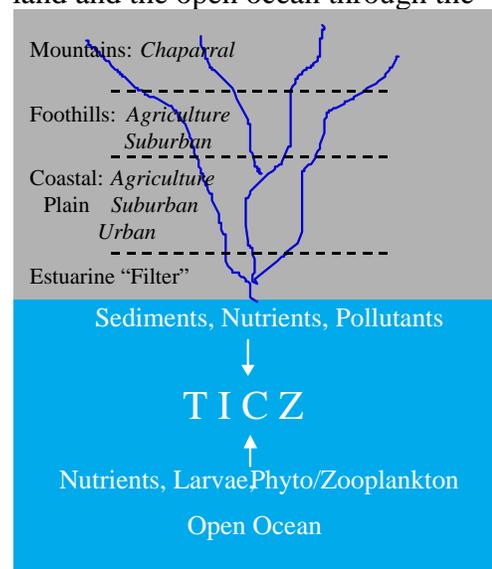


Figure 1. Terrestrially Influenced Coastal Zone

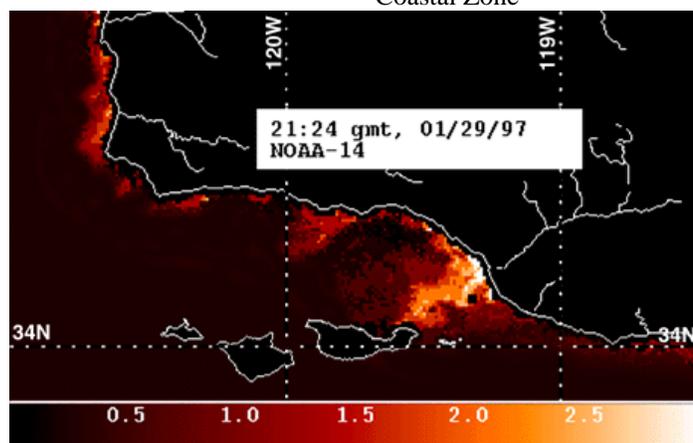


Figure 2 -- Sediment plumes in LTER region

The second hint of a strong terrestrial influence on coastal reefs comes from seasonal nutrient data. Nutrient concentrations (uM) typically are quite low except during winter and some springs, the periods when most measurable rain falls in the region (Fig 3). During the winter/spring peaks, nutrient concentrations at sites in the channel reach levels comparable to those found in intense upwelling zones of Central and Northern California. The source of this pulse of nutrients in winter is not presently known, but the coincidence between the pulse in nutrients and the peak in run-off poses the hypothesis that the pulse is at least partly of terrestrial origin. Interannual variation is also substantial in both the size of the nutrient peak and its breadth. This time series includes both an intense El Niño (1998) and La Niña (1999). The relative contributions of interannual variation in rainfall/watershed processes versus interannual variation in ocean processes to these nutrient dynamics is unknown.

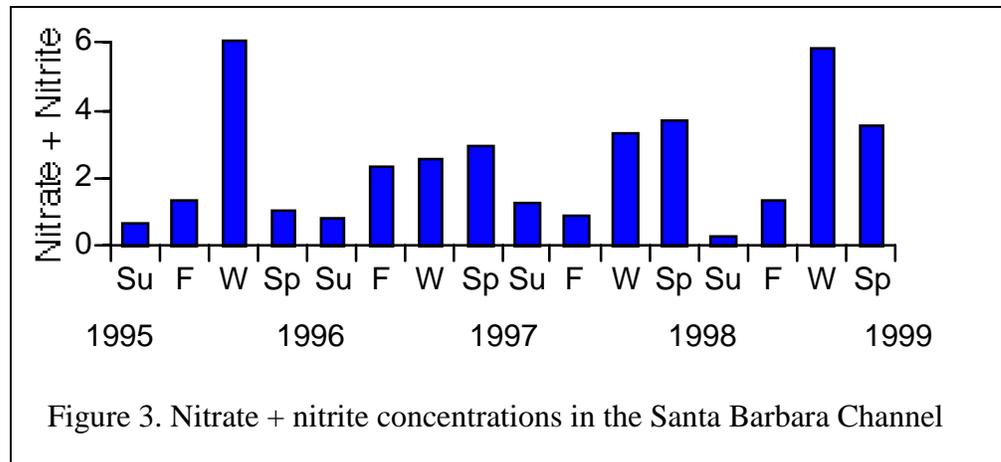


Figure 3. Nitrate + nitrite concentrations in the Santa Barbara Channel

#### NEED FOR A KELP FOREST LTER

Our choice of kelp forests as the ecosystem of study in semi-arid regions stems not only from their high ecological and economic importance, but also from their commonness; kelp beds predominate on shallow temperate reefs throughout the world, covering an area that is comparable to that occupied by coral reefs. The addition of a kelp forest LTER would add representation of an ecosystem with a broad geographic domain to the LTER network. Three additional features support studying land/ocean interactions in this ecosystem in the context of the LTER program.

*Contrasting Positive and Negative Watershed Influences:* As noted above, the constituents of terrestrial runoff can have both positive and negative consequences for marine organisms on rocky reefs. Some constituents will act as agents of disturbance (e.g., sediments, pollutants). Other constituents may have positive effects on individuals through subsidies of trophic interactions (e.g., nutrients). How these positive and negative effects interact, and more importantly how the nature of their interaction scales with discharge events of different sizes, is largely unknown. These influences can only be teased out in a long term study that examines community responses to a wide range of events.

*Distinctive Trophic Structure:* Kelp forest communities are extremely diverse and are characterized by a trophic structure that is unique to shallow reef ecosystems (Figure 4). Unlike competition in most other ecosystems,

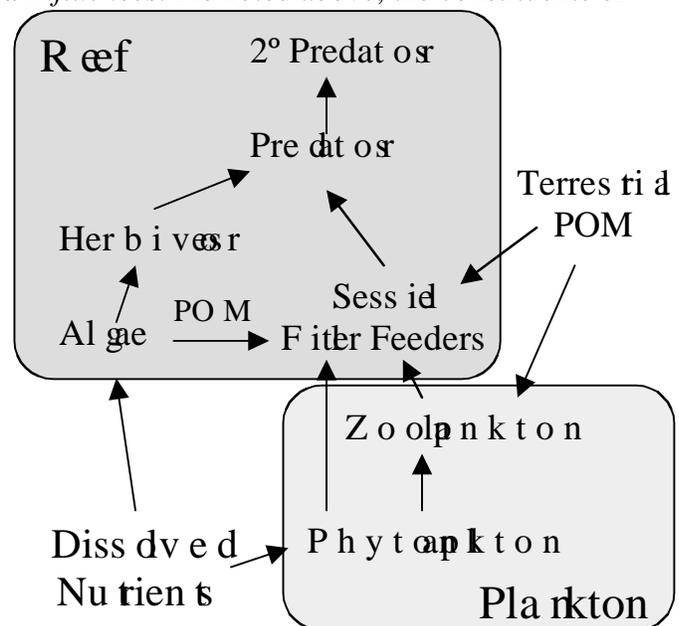


Figure 4 Simplified coastal food web

this competition occurs *between* different trophic levels. The sessile invertebrates are consumers, who obtain their nutrition by filtering plankton and particulate carbon from the water column over the reef. The macroalgae are primary producers who derive their nutrition from dissolved nutrients. Competition between sessile invertebrates and macroalgae can be mediated by the relative supply of nutrients and particulate organic matter to the reef. Both the ocean and runoff serve as sources of these resources (Figure 4). Substantial changes in the relative supply of these resources due to the interaction of the ocean processes and runoff have the potential to alter reef community structure significantly.

As diagramed in Figure 4, nutrients can be consumed by macroalgae directly or they can enter the reef system through phytoplankton. Nutrients consumed by one form of primary producer (e.g., phytoplankton) will be unavailable to the other (e.g., macroalgae). In addition, augmentation of the delivery of POM through terrestrial runoff would favor sessile invertebrates. Processes that favor one pathway over another could have dramatic effects on the structure of these communities.

*An Ecosystem in Transition:* Reef communities along the California coast have changed substantially in recent decades and other major biological changes appear on the near horizon. Some of the changes appear to have climatic links; others are tied to biological shifts. On the climate change side, there has been a gradual increase in sea surface temperature in this region over the past century, which has been accompanied by lower production (McGowan et al. 1998). In addition to these long term trends, there are more abrupt changes among years and decades.

We have documented ecosystem changes associated with this warming at the decadal scale. We have seen shifts to dominance by southern species in kelp forest fish at two sites in southern California, including one in the Santa Barbara Channel (Fig 5; Holbrook et al. 1997). Since the early 1970's, the proportion of species in fish assemblages that are cold-water, northern species

has dropped by about half, while the proportion of southern, warm-water species has increased nearly 50 percent. Overall, there has been a substantial decline in total fish abundance, which correlates closely with declines in productivity (Holbrook et al.

1997). These patterns suggest an ongoing redistribution of marine species along the coast of California that is consistent with

predicted northward shifts in species' ranges in response to ocean warming. Such shifts would be similar to those observed in terrestrial habitats for the Edith's checkerspot butterfly (Parmesan 1996).

Another major change facing Southern California kelp communities is the re-colonization of sea otters, a keystone predator in kelp forest ecosystems in the NE Pacific (VanBlaricom & Estes 1988). Sea otters once ranged around the Pacific from northern Japan to central Baja California, but were hunted to extinction throughout most of their natural range (including southern California) by the beginning of the 20<sup>th</sup> century (Keyon 1969). In the last couple of years, groups of otters have started foraging south of Pt. Conception in the Santa Barbara Channel. The number of otters in the channel is increasing rapidly, and it is likely that resident otters soon will be common throughout the region. Documenting ecosystem changes in response to the re-colonization of this keystone predator offers a unique opportunity for our proposed LTER site.

#### REGIONALIZATION AND SITE SELECTION

The Santa Barbara Channel is a convenient LTER site for the large number of investigators collaborating on this proposal, but our choice of the Santa Barbara Channel was not based on

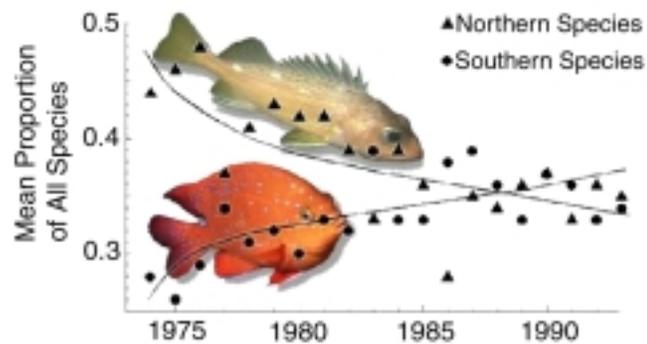


Figure 5. Changes in fish species composition in So. California Kelp Forests

convenience. Rather, the Santa Barbara Channel is the *ideal* site for a coastal LTER. Here is a brief list of some of the more compelling reasons:

I. COASTAL OCEANOGRAPHY – The primary source of *ocean derived* nutrients near the coast is upwelling. The extent of upwelling varies considerably along the west coasts of North and South America. If nutrient inputs from land play a significant role in coastal production anywhere, their influence should be greatest in regions with limited ocean sources of nutrients. Major upwelling does not occur off most of southern and Baja California, including the Santa Barbara Channel. As a result, surface waters in the region are commonly warm, saline, and nutrient poor.

II. RICH DIVERSITY OF WATERSHEDS, LARGE SPATIAL/TEMPORAL VARIATION -- The Santa Barbara Channel offers a rich diversity of watersheds for experimental and observational study that typify the types of watershed found in most Mediterranean climates. About 40 catchments drain into the Santa Barbara Channel from the coast range called the Santa Ynez Mountains. Steep montane slopes composed of readily eroded material and strongly seasonal rainfall create potentially large sources of sediments. The intermittent occurrence of fire in the catchments further enhances temporal variation in the export of sediments and nutrients. The catchments of the Santa Barbara region vary widely in the proportion of agricultural and urban development, which differentially contribute nutrients and pollutants to the runoff. Modifications of the frequency or intensity of droughts due to climate change or ENSO events will be strongly expressed in the Mediterranean climate of our region. Hence, the spatial and temporal variation in climatic and landscape conditions in the upland catchments provide a unique opportunity to assess the diverse effects of terrestrial inputs on kelp forests.

III. STRONG EL NIÑO SIGNATURE -- The Santa Barbara Channel is a site of dramatic physical and biological responses to El Niño Southern Oscillation (ENSO) events. Terrestrial runoff and the associated transport of sediments, nutrients, and pollutants increase dramatically because of elevated precipitation during ENSO events. Sea surface temperatures increase and offshore nutrient levels decline as the thermocline deepens. Large scale patterns of ocean circulation also change dramatically, and storm disturbance from waves is often extreme. Corresponding to these physical changes are dramatic biotic changes including: northward range extensions, precipitous declines in the giant kelp *Macrocystis pyrifera*, and unusual changes in the abundance of many species of algae, invertebrates and fish (Tegner & Dayton 1987, Dayton & Tegner 1989)

IV. SPECIES INTERACTIONS HAVE BEEN STUDIED EXTENSIVELY – Kelp forests in the Santa Barbara Channel have been the focus of extensive experimental/observational studies by UCSB researchers over the past 30 years (e.g. Neushul et al. 1967, Foster 1975a, b, Ebeling et al. 1980, 1985, Reed 1990 a, b, Reed et al. 1988, 1997, 1998, 1999, Schmitt & Holbrook 1986, 1990a, b, Holbrook & Schmitt 1988, 1989 ). Although terrestrial influences on the system are poorly understood, the nature of species interactions is well known for many of the dominant taxa.

V. MAJOR BIOGEOGRAPHIC BOUNDARY – Pt. Conception, at the western boundary of the Santa Barbara Channel, is a major biogeographic boundary for a wide variety of marine taxa (Valentine 1966, Briggs 1974). Such a location may be particularly sensitive to shifts in species composition driven by climate. An LTER that abuts this sharp transition zone offers the unique opportunity to study the dynamics of a boundary between biogeographic provinces.

VI. COLLABORATION WITH OTHER LONG-TERM RESEARCH PROGRAMS – A Santa Barbara Channel LTER would be embedded within a large number of ongoing, long-term research efforts (see appended letters of support). These include:

- The Channel Islands National Marine Sanctuary and Channel Islands National Park both have ongoing monitoring and research programs in kelp forests (16 sites since 1982). They are enthusiastic about collaborating with us on LTER sponsored projects.
- The University of California manages an extensive collection of natural reserves within its systemwide UC Natural Reserve System whose purpose is to enhance teaching and research. Three coastal reserves would be included in the proposed LTER site (Carpinteria salt marsh, Coal Oil Point, and Santa Cruz Island), each of which has a resident reserve manager and

ongoing monitoring that is funded by the University of California. Restricted public access to these reserves makes them ideal sites for long term ecological studies.

- The Minerals Management Service funds a large study of ocean circulation in the Santa Barbara Channel region. The program is run through Scripps Inst. of Oceanography and includes extensive arrays of moorings to measure and ultimately model ocean circulation in this region. In addition, MMS supports Dugan's research on the responses of higher trophic levels (shorebirds) to invertebrate prey living in kelp wrack on exposed sandy beaches in Santa Barbara County.
- Santa Barbara County spends \$400,000 to \$900,000 per year collecting field data and performing chemical analyses on creek and ocean waters for seven watersheds in the Santa Barbara County. They are very enthusiastic about our efforts to establish a Land/Ocean LTER site in Santa Barbara and have offered to give us access to all County data regarding stream hydrology and material transport from watersheds to the coast.
- NASA funds a long-term (>6 y) study at UCSB that investigates marine plankton blooms associated with runoff (hereafter referred to as Plumes and Blooms). The goal of this project (awarded to Seigel, Brzezinski, Mertes, and Wasburn) is to develop new satellite ocean color algorithms to use in coastal waters influenced by terrigenous materials (sediments, dissolved organic materials, etc.). *In situ* optical quantities and in-water constituents are collected every two weeks along a 7 station transect crossing the Santa Barbara Channel and related to simultaneous ocean color images from the SeaWiFS satellite sensor.
- A new, multi-million dollar long term grant was recently awarded to Gaines and Warner by the Packard Foundation to examine changes in marine communities in response to changes in ocean circulation along the west coast of the US. UCSB is one of the hubs of this project. This new project will be tightly linked with the Santa Barbara LTER and will fund much of the background monitoring of ocean circulation and species changes that would otherwise have to be funded by NSF (see Section 6 - Budget for details of this matching funding).

VII. EXISTING TIME-SERIES DATA ARE EXTENSIVE -- Time series of a wide range of physical and biological data exist for both uplands and the Santa Barbara Channel. Upland data include rainfall, runoff, and GIS based land cover. Ocean data include long term records on temperature, wave heights and direction, and ocean color. Biological data include abundances of a wide range of invertebrate, vertebrate and algal species including records of different life stages (e.g., adult, juvenile, young-of-year, and larvae/spore), trophic levels (primary producers to tertiary consumers), food webs (i.e., those coupled to benthic or pelagic primary production) and habitats (e.g., hard and soft bottom, inter- and subtidal, benthic and pelagic). Primary sources of data include: (1) county and federal (National Park Service, Minerals Management Service, NOAA) agencies; (2) UCSB scientists; and (3) California Cooperative Oceanic Fisheries Investigations (CalCOFI) which have been collecting abundance data on phytoplankton, zooplankton, fish and birds quarterly in the Channel since 1949.

VIII. UNPRECEDENTED LONG TERM CLIMATE RECORD -- The varved sediments of the anoxic deep basins of the Santa Barbara Channel offer one of the highest resolution data sets of climate change over the past 100,000 years (Schimmelmann et al. 1990; Kennedy and Brassell 1992; Behl and Kennett 1996). These records show a strong connection between local climate changes affecting the Santa Barbara Channel and global changes in ocean circulation. They also include records of biotic changes over the same time scales for several taxa (Baumgartner 1992). These records provide an unmatched opportunity to place fluctuations observed at the proposed LTER sites in the context of much longer records.

#### **PROPOSED STUDY SITES**

Rather than focus on a single watershed, with its inherent peculiarities, our proposed LTER site encompasses several coastal watersheds that drain into the Santa Barbara Channel. The geographical extent of the site is bounded by the Transverse Ranges of central and southern California to the north, the Channel Islands to the south, Pt. Conception to the west, and the Santa Clara River to the east (Fig 6). We will focus on 3 primary catchments (Carpinteria,

Goleta, Alegria) with less intensive studies of 10 additional catchments (Bulito, Gaviota, San Onofre, Quemado, Refugio, Capitan, Burro, Mission, Rincon, Willow) and 2 rivers (Ventura and Santa Clara) to allow regionalization of measurements and modeling.

The 3 focal catchments were chosen based on several criteria: (1) existence of kelp beds near their mouths, (2) a range of land uses that encompasses undisturbed montane, rural, agricultural, suburban and urban environments, (3) relatively short drainages so we can study the entire watershed, (4) the existence of detailed GIS-based topographic, climatic, land cover and land use information, (5) controlled access to the sloughs and mouths, (6) recent gauging records and/or gaugable flows, and (7) distributed rainfall gauges with long historical records. Extensive kelp forests at the three focal sites extend to ~ 15 m depth. Each occurs on a gently sloping, low relief, shale reef that is predominately exposed to N and W swells.

The Carpinteria Saltmarsh watershed is drained by two major streams: Santa Monica Creek drains a basin of 16 km<sup>2</sup>, and Franklin Creek drains a basin of 11 km<sup>2</sup>; both begin at an elevation of 530 m (Page et al. 1995). Flows from smaller creeks drain an additional 3 km<sup>2</sup>. Mountains and foothills in the watershed are largely sedimentary rock and are covered by chaparral that grades into avocado orchards, open agricultural fields, greenhouses and urban development in the foothills and coastal plain. The watershed empties into a 0.9 km<sup>2</sup> estuarine wetland that is part of the UC Natural Reserve System. Jetties at the inlet help maintain year round tidal flushing.

The Carpinteria Saltmarsh watershed is drained by two major streams: Santa Monica Creek drains a basin of 16 km<sup>2</sup>, and Franklin Creek drains a basin of 11 km<sup>2</sup>; both begin at an elevation of 530 m (Page et al. 1995). Flows from smaller creeks drain an additional 3 km<sup>2</sup>. Mountains and foothills in the watershed are largely sedimentary rock and are covered by chaparral that grades into avocado orchards, open agricultural fields, greenhouses and urban development in the foothills and coastal plain. The watershed empties into a 0.9 km<sup>2</sup> estuarine wetland that is part of the UC Natural Reserve System. Jetties at the inlet help maintain year round tidal flushing.

Goleta Slough watershed encompasses an area of 123 km<sup>2</sup> and is drained by seven streams originating near the crest of the Santa Ynez Mountains at about 1000 m that merge into three streams before entering the slough. All pass through a 0.7 km<sup>2</sup> estuary (a State Ecological Reserve) before entering the ocean adjacent to the campus of UCSB. The Goleta watershed is composed of three regions (alluvial plains, foothills, and mountains) distinguished by topography and land cover and use. The gently sloping alluvial plain contains intensive residential and commercial development covering most of the land and has channelized stream courses. In the moderately sloping foothills avocado and citrus orchards are the dominant land use and some modification of stream courses has occurred. The montane terrain has avocado farming and cattle ranching in the lower elevations and largely undeveloped private and National Forest lands supporting native chaparral with natural riparian corridors at higher elevations.

The Alegria catchment lies within Hollister Ranch, a large private holding largely undeveloped and managed as a cattle grazing cooperative with some 100-acre parcels occupied by houses. The owners association has encouraged our use of the catchment for research, which will benefit from limited public access. Alegria beach has been the site of experimental ecological research by Gaines, Reed, Holbrook and colleagues for the last four years, and UCSB's Museum of Systematics and Ecology has recently completed a thorough botanical survey of the whole Ranch. Vegetative cover in Alegria catchment is typical of the stretch of coast west of Goleta to Pt. Conception, with mixed grasslands from the ocean to 500 m and coastal scrub and chaparral with scattered oak forests up to the ridge line at 1000 m. Riparian woodlands border Alegria Creek, and a small estuary characterized by *Ruppia cirrhosa* and supporting a population of Tidewater Goby, an endangered fish, lies at the seashore.

## PROPOSED RESEARCH

The research we propose addresses questions and hypotheses related to all five core areas of research topics shared by LTER sites. The key issues that we will specifically address are (1)



Figure 6 -- Map of Santa Barbara LTER site.

spatial and temporal scales over which terrestrial runoff and ocean forcing perturbs kelp forest ecosystems, (2) patterns and processing of organic matter in the ecosystem, (3) patterns of organic and inorganic inputs and their movement from the land to the coastal zone, (4) the effects of terrestrial runoff on patterns and controls of primary production in kelp forests, and (5) the effects of terrestrial runoff on the long-term population dynamics of key kelp-forest species and on trophic interactions. Below we provide background information, specific questions that will be addressed, and the approach to be taken to address these issues.

### *1. Transport and Processing of Nutrients and Sediments from Watershed to Ocean.*

Background: Fluvial transport and processing of nutrients, organic matter, and sediment are the primary means by which land masses influence coastal ecosystems. The volume and geophysical/chemical properties of runoff are determined by the amount and pattern of rainfall, terrain, lithology, land use, vegetation, and perturbations to the watershed and adjoining estuary. For example,  $\text{NO}_3^-$  is the primary inorganic N form from forested and agricultural catchments, whereas  $\text{NH}_4^+$  is often high in urbanized areas (Gabric and Bell 1993, Howarth et al. 1997). The watersheds feeding into the Santa Barbara Channel are complex with a mix of land uses and nutrient and sediment sources to streams; thus there is a mix of processes controlling those inputs. Most drainages start in the mountains, which are generally in chaparral and coastal sage scrub, and burn episodically (Fig 1). The foothills are a mix of grazed grassland/oak woodland, agricultural land, and suburban development. Lower yet, the coastal plain includes foothill land uses, but also urbanized areas. Finally, there are the coastal marshes, sloughs, or lagoons. The nature of inputs varies across these zones and land use patterns, as do the processes driving inputs. The main disturbances are fire, grazing and flooding, all of which are common in coastal areas with Mediterranean climates. Such perturbations can have catastrophic effects on kelp forest ecosystems. Cuyler Harbor on San Miguel Island rapidly filled in due to sedimentation resulting from wholesale erosion after overgrazing by sheep (Johnson 1980). The large kelp bed shown in earlier (1871) maps of the harbor no longer existed by 1895. Less catastrophic runoff effects such as increased water column turbidity and/or nutrient inputs occur more frequently and can alter primary production in kelp forests, with cascading effects on coastal food webs. Urban development and agriculture in the flood plain can fill estuaries with sediment, reducing their filtering capacity and increasing material delivery to the sea. The effects of such processes can be assessed on the time scales of an LTER. Processes within watersheds may be complex and result in extensive modification of inputs to stream systems. Nitrification, denitrification and mineralization of organic N occur as the nitrogen crosses the ecotone from the land to stream or wetland (Meyer et al. 1988, Triska et al. 1989, Chesterikoff et al. 1992, Bradley et al 1995). Thus the potential for terrestrial runoff to influence kelp forest ecosystems in the Santa Barbara region is large, and the extent of this influence will vary over space and time.

Focal Questions: *How does the spatial scale of terrestrial influence on the coastal zone vary with watershed size, history (i.e. fire, grazing), land-use, and filtering capacity of the wetland? Do nutrient and sediment inputs to the coastal ocean vary non-linearly as a function of discharge and land use in a catchment? Do anthropogenic inputs dominate nutrient and sediment loads within stream channels? Do natural inputs dominate only following major disturbances (i.e., fire and floods)? Do riparian and in-stream processes play any significant role in controlling the balance of inputs to the stream and outputs to the coastal oceans?*

Approach: Evaluating the net sources of sediment and nutrients to the coastal ocean requires a hierarchical approach that starts at the scale of regional analysis and moves to identifying sources and controlling processes within catchments. Regional studies will combine measurements in the 3 core watersheds with surveys of 10 additional streams and 2 rivers to validate and extend these studies. We will then scale down into individual watersheds and to studies on those processes that appear to be critical in controlling overall export to coastal waters. We have six specific objectives that will help resolve our focal questions.

- 1) Evaluate the amount of runoff and export of sediments, nutrients and organic matter (OM) from catchments with differing geomorphic and land-use characteristics.
- 2) Identify which geomorphologic zones supply the main inputs of nutrients and sediments.

- 3) Evaluate how this varies seasonally.
- 4) Identify the specific land use types that cause the inputs.
- 5) Assess the processes controlling OM, nutrient & sediment yield from each land-use type.
- 6) Assess the roles of riparian & in-stream processing of nutrients, organic matter, & sediments.

#### REGIONAL SCALE STUDIES:

This approach will combine a set of measurements of discharge from the focal and supplemental watersheds with modeling of solute and sediment-discharge relationships. The models will be driven by data on hydrology and land use in the different catchments. With data from this project, the models will provide information critical to evaluating the role of terrestrial systems as nutrient, OM, and sediment sources to coastal systems under changing climate and land use patterns. We will collect the following data:

- 1) We will generate stage-discharge rating curves using pressure transducers, current meters and tracer dilution techniques. USGS currently maintains a gauge on one of the major streams entering Goleta Slough as well as on two other local streams and both rivers. Moreover, intermittent discharge records exist for 16 streams over the last two decades.

- 2) We will collect rainfall data at all sites. About 80 rainfall gauges distributed at all elevations with 25 to 50 years of records exist for our primary study area.

- 3) During a range of flow conditions, including floods, we will make direct measurements of currents, nutrient, and sediments in accessible cross-sections near the mouths of the estuaries. At our Goleta slough core site, we will mount an electromagnetic current meter on an existing structure near the mouth of the slough to monitor tidal exchanges.

- 4) In the core watersheds, we will carry out regular measurements of discharge-stratified runoff, nutrients, and sediments. These will include both flood and low flow periods. We will sample during storm runoff by using both automatic samplers and teams of people. Event sampling of rain will be done with collectors designed to open only during rainfall.

The following analyses will be performed on all water samples: a) Dissolved inorganic ( $\text{NO}_3^-$  and  $\text{NH}_4^+$ ) and organic nitrogen, particulate nitrogen, natural abundances of nitrogen isotopes; b) Soluble reactive phosphorus, dissolved organic phosphorus and particulate phosphorus; c) Particulate and dissolved organic carbon; d) Total suspended sediments and size fractionations.

By sampling our 3 core watersheds intensively and the supplemental sites regularly over years with different climates (e.g. El Niño/La Niña), we will be able to calibrate and test a set of rainfall-runoff and nutrient/sediment export models, which can then be used to predict inputs to coastal systems across changing climate and land use in the region. The investigators focused on this aspect of the project (i.e., Melack, Cooper, Page, Dunne, Mertes, Keller, and Clarke) have considerable experience performing all the appropriate work (see CVs). Once a model has been developed and validated, we will develop predictions of flow of nutrients/sediments with probability distribution functions (pdfs) of rainstorm intensity, duration, and spatial extent. The pdfs will be derived from available radar and ground-surface instrumentation. This stochastic approach to predicting flow will be combined with models relating flow to sediment and nutrient loading (developed from our measurements) to estimate patterns of nutrient and sediment supply under a range of climate and development scenarios. Our approach is similar to export coefficient modeling (e.g., Johnes 1996) and depends on (1) sampling within catchments or subcatchments with different land uses and land cover (part of the watershed scale studies), (2) data on demographics and economic activity available from local agencies and (3) detailed GIS of the landscape. We have assembled a GIS database for the proposed LTER area, including all coastal watersheds, with high resolution versions for our core watersheds. This database includes DEMs, precipitation and river gauge data, soil cover, fire history, and landcover maps.

We will work with three hydrological models to find the one that can be calibrated and linked to nutrient and sediment generation most efficiently. The models vary in their resolution of runoff physics and therefore their input data requirements. The models are: (1) the urban form of the Soil Conservation Service (SCS) TR55 (SCS 1986); (2) the continuous runoff simulation model HSPF (Johanson et al. 1980) as supported by the EPA Center for Exposure Assessment Modeling; and (3) the kinematic-wave runoff model KINEROS (Woolhiser et al. 1990). We

have successfully applied the SCS TR55 model to calculate runoff from the Goleta watershed, and have added sediment, nutrients and pollutant export to a version of the model. Further, we have written AML software for Arc/Info/Grid to model runoff from homogeneous subcatchments. This software uses high-resolution DEMs and interpolates rainfall surfaces based on elevation and the radar signature of rainfall intensity (which we will calibrate from our rain gauges and existing stations). Preliminary results based on tools developed by Mertes show estimates for storm event discharge within 10% of those measured for the Sespe Creek watershed, a tributary of the Santa Clara River. Estimates of soil erosion from surface runoff based on the revised universal soil loss equation (Roo et al. 1989) agree with the relative scale of coastal plumes for Santa Cruz and Santa Rosa Islands. Together with the routinely available runoff-modeling codes and our functions relating flow to constituent concentrations, our software can be used efficiently to calculate the coastwide export of materials to the sloughs and ocean under a range of environmental and development scenarios.

#### WATERSHED SCALE STUDIES:

At this scale, we will work only in the 3 core watersheds (Carpinteria, Goleta, and Alegria), with the key issues being to identify the major sources of nutrients, OM, and sediment, and to identify the major processes supplying materials (e.g. natural processes vs. fertilizer  $\text{NO}_3^-$  vs. direct waste input of  $\text{NH}_4^+$ ). We will apply an approach similar to that being used by Page (1995) in the Carpinteria watershed. This combines available GIS-based watershed scale data on land use cover (e.g., urban, greenhouses, open field, orchard), nutrient concentrations, and stable isotope analyses to evaluate the importance of different factors in controlling export into coastal waters. For example, N in waters derived from human and animal wastes are enriched in  $^{15}\text{N}$ , while nitrate in synthetic fertilizers is depleted in  $^{15}\text{N}$  (Kendall et al. 1995, McClelland et al. 1997, Page 1995). The effect of agriculture on the creeks draining into Carpinteria marsh is dramatic. Nitrate-N concentrations in one of two creeks that supply ~90% of the freshwater to the marsh, increase 10 to 100 fold as this stream crosses the coastal plain (Page et al. 1998). Data on  $\text{NO}_3^-$  and  $\text{NH}_4^+$  concentrations indicate that  $\text{NO}_3^-$  is the principal form of inorganic N entering the marsh and exported to the coastal ocean (Page et al. 1995).  $\delta^{15}\text{N}$  values at the marsh outflow indicated that the  $\text{NO}_3^-$ -N exported from the marsh comes primarily from the major creeks.

We will analyze nutrient concentrations and isotopic signatures of N in various forms at key locations in the core watersheds. We will evaluate the role of different contributors to the signal at the river outflows by sampling sub-catchments to examine particular land uses and landscape signatures. We will sample above and below the landscape unit, e.g., grazed pastures, avocado orchards, residential neighborhoods, native chaparral, etc. Then, by using mixing models we will evaluate the importance of different sources to the higher order reaches. We will base these mixing models on source area estimates generated from GIS analysis of each watershed.

We will conduct exploratory studies to determine if it is feasible to identify pollutant sources by using exotic organic compounds and microbes. Organic pollutant inputs (e.g., pesticides, PCBs, and petroleum derivatives) vary with land use (Gilliom et al. 1999). We will measure concentrations of organic pollutants (using GC-MS in Holden's lab) in runoff and coastal water. Sediment fluxes during storms carry non-indigenous microbes to coastal waters, and we will test the applicability of using microbial fingerprints as indicators of sediment and pollution sources. Fingerprinting will be coupled to watershed-scale, GIS-based models incorporating land use and soil conditions to evaluate input sources to streams (Fraser et al. 1998, Irvine & Pettibone 1996). We will use denaturing gradient gel electrophoresis (DGGE) of 16S rDNA to analyze microbial communities in different source areas (e.g. agricultural vs. urban) and in outflow waters. DGGE has been shown to be sensitive to changes in bacterial community structure along a hydrochemical gradient (Torsvik et al., 1998). Holden has been developing this approach and has the necessary experience in both watershed modeling and DGGE.

#### SITE AND PROCESS STUDIES

The above work will provide an adequate picture of the main sources of nutrients, OM, and sediments to streams. However, these approaches have limitations for quantifying the processes

driving nutrient generation and processing within catchments. Physical and biological processes fractionate N and can confound accurate quantification of particular sources (Kendall 1998). Thus, a full understanding of nutrient and sediment yield to coastal systems requires more site focussed process measurements. Some of the experimental work will begin early in the project, while other work will develop as the watershed scale work identifies the critical processes. One process we believe is important to study is fire and its effects on nutrient and sediment generation. Large fires occur regularly (site return frequency of 50-80 years; Keeley et al. 1999), and we will take advantage of either large controlled burns (US Forest Service carries these out) or natural fires to establish studies on fire dynamics. Site based studies will target several specific questions about the generation and consumption of nutrients and OM. We have currently identified three key areas that we know are important in controlling nutrient and sediment generation and so require study as part of this project: 1) Processes affecting groundwater  $\text{NO}_3^-$ ; 2) The role of stream channel processes in sequestration/mobilization of nutrients & sediment; 3) The role of estuaries/marshes as biofilters.

1)  $\text{NO}_3^-$  concentrations can be up to 80 ppm in soil solution in oak-grass communities, while groundwater concentrations average around 8 ppm and streamwater closer to 2 ppm (Schimel, unpublished data). It is unclear what causes this dramatic decline along the flowpath, or how general the pattern is. There are several possible explanations: mixing with other,  $\text{NO}_3^-$ -poor water sources, plant uptake, and denitrification. We will establish lysimeters and piezometers to sample soil- and ground-water in transects away from stream channels. These will initially be established in upland chaparral (Los Padres National Forest) and in oak woodland/grassland (Alegria). We will also find agricultural and urbanized sites where we can establish samplers. We will collect water samples regularly (at least every two weeks through the wet season) and will analyze them for the full suite of nutrients, DOC, and DON. We will also regularly analyze the isotopic composition of  $\text{NO}_3^-$ . Shifting concentrations coupled to the  $^{15}\text{N}$  data should identify the importance of denitrification in consuming groundwater  $\text{NO}_3^-$ . If denitrification is important, groundwater  $\text{NO}_3^-$  should be  $^{15}\text{N}$  enriched. These measurements will also provide input data on the concentrations and isotopic signatures of groundwater entering the stream system from various sources; this will help validate the watershed analyses. By coupling nutrient concentrations with hydrological models, we will be able to model the movement and fate of  $\text{NO}_3^-$  as it moves through groundwater. The hydrological approaches to analyzing soil column processes will be coupled to in situ assays and lab studies on N mineralization, nitrification, and denitrification; using standard approaches (Weaver et al. 1994, Clein and Schimel 1995, Davidson and Schimel 1995). Schimel's lab has wide experience in these kinds of studies at the Bonanza Creek LTER (see prior support) and is carrying out very similar studies combining lysimetry, piezometry, and soil biology to evaluate N dynamics in the Santa Ynez Valley.

2) A second important area of process studies is in-channel processes that may sequester and transform nutrients and sediment. Many of the creeks in the Santa Barbara area go through regular cycles of algal and plant growth and scouring. In their open, lower reaches, creeks develop algal communities every summer that are scoured by winter flows; on a longer time scale, thick riparian vegetation (willow, papyrus, cattails, etc.) develops which is scoured by floods that deposit the material downstream and in coastal systems as coarse detritus. The last major scouring occurred during the winter of 97-98 and so this is a good baseline year for studying the development of riparian communities. This vegetation also acts as a sediment trap. Nutrient immobilization by decomposers and denitrification in the hyporheic zone may be other  $\text{NO}_3^-$  sinks. Thus, climate variability and in-stream processes may be important in controlling inputs to coastal systems. Therefore, we will measure and evaluate several processes, initially in small scale experimental studies. Subsequent studies may involve larger manipulations of stream channels, such as removing riparian vegetation. As it is likely to take at least 6 months to a year to get necessary permits for such work, we will only develop such experiments after the initial process studies identify the need. The core set of studies will include:

a) Stream channel/riparian productivity: We will establish replicate plots along each stream in each of the main geographic zones (mountains, foothills, plain, and estuary). Algal productivity will be measured by light/dark chamber  $\text{CO}_2$  fluxes and  $^{14}\text{C}$  uptake. Algal biomass will also be

measured. These measurements will provide estimates of nutrient uptake rate (productivity/C:N ratio) and of total sequestration. Vascular plant production will be assayed using standard methods (harvests for small plants and allometry for trees), with nutrient analysis to evaluate uptake. Productivity of each component of the system will be related to stream conditions, light levels, nutrient supply, etc.

b) Control of algal productivity: In small stream channel experiments, we will carry out manipulations (shade/fertilization) to evaluate the controls on algal productivity and nutrient uptake. These will be carried out in each of the major geographic zones.

c) Nutrient uptake lengths (Fisher et al. 1998) in different stream regions: This will involve the application of a  $^{15}\text{NO}_3^-$  tracer to stream reaches in the major zones and in different seasons. The  $^{15}\text{N}$  will be followed downstream as  $\text{NO}_3^-$  as well as being traced into different components of the stream ecosystem to critically evaluate the fate of  $\text{NO}_3^-$ . These experiments will be done several years into the study and at a place and time to limit the “damage” done by tracer studies on our ability to use  $^{15}\text{N}$  natural abundance analyses.

d) The role of stream detritus in nutrient immobilization. Both leaf litter and coarse debris have the ability to immobilize nutrients in streams, for varying lengths of time. We will estimate litter inputs and decomposition to estimate their potential for nutrient immobilization and release.

e) Denitrification in riparian soils and hyporheic sediments. We will use the intact core acetylene reduction assays (Davidson and Schimel 1995) as our primary measure of total denitrification. We will also use flux chambers to estimate  $\text{N}_2\text{O}$  fluxes in the riparian zone.

f) Food web dynamics: Work in coastal California streams has shown that top predators, such as trout, can have large effects on the abundance and distribution of lower trophic levels (Cooper 1988, Wiseman et al. 1993, Power 1990). In whole-pool experiments, Cooper et al. (1986) found that adding trout decreased invertebrate predators and increased in grazers. Further, microcosm experiments showed that grazers have large effects on algal biomass and species composition (Dudley and D’Antonio 1991, Sarnelle et al. 1993). Because algae are major consumers of nutrients, these indirect effects of trout may have effects on nutrient spiraling. Furthermore, these effects on nutrient spiraling may change with climatic and hydrological regimes. We will measure nutrient pools in different trophic compartments (e.g., algae, leaf litter, invertebrates at different trophic levels, fish) in streams containing and lacking trout. There is a mosaic of streams and stream reaches containing or lacking trout that have been extensively studied by Cooper and associates (cited above). As a consequence, we will be able to use this preexisting, natural experiment to incorporate a better understanding of stream food web dynamics as controls on nutrient retention in streams.

3) Marshes/Sloughs as biofilters. Although there are few remaining marshes in Southern California, several creeks in the Santa Barbara area have sloughs or marshes at their mouths. The watershed scale analyses will permit some estimate of the ability of these systems to act as biofilters under different weather conditions. Maximal filtering capacity is likely during the summer, when low flows limit nutrient exchange and plant growth is rapid. During major floods the effective filtering ability of these systems may be very low. We will begin measurements of plant productivity and of denitrification rates in the estuaries to complement the watershed analyses, providing an initial analysis of processes driving biofiltering ability. As we develop a better picture of the dominant processes affecting nutrient flux, we will develop further work on important processes. Further, we expect the extent of tidal flushing of Goleta Slough to be increased within the next three years by modification of diversion structures within the slough. This modification will serve as an experiment to aid our analysis of the role of coastal wetlands in modifying exchanges with the ocean.

## *2. Spatio-temporal extent of terrestrial exports to the coastal reef ecosystem.*

Background: The timing, spatial extent, and residence time of runoff in the coastal zone are influenced not only by seasonal and interannual variability in runoff, but also by coastal currents that vary with tidal cycle, wave climate, season, and interannual variability in large scale ocean forcing. Thus there is a high potential for the effects of runoff on coastal reef communities to be influenced by ocean processes. Consequently, the potential effects of runoff on kelp forests are

likely to vary in different ocean domains (southern vs. northern California) and in different oceanic climates (i.e. ENSO vs. non-ENSO years).

**Focal Questions:** *Over what spatial and temporal scales does watershed runoff influence the coastal zone? What is the relationship between nutrient levels in the coastal zone and the magnitude of terrestrial inputs? What are the temporal patterns of POM and nutrient delivery from terrestrial and marine sources to coastal reefs? Does the relative importance of terrestrially derived nutrients increase in El Niño years when rainfall is typically high and ocean nutrients are depressed?*

**Approach:** An important first step to assessing the extent of terrestrial exports to coastal reefs is a characterization of the temporal variation in nutrient, sediment, and POM dynamics at both regional and site specific scales. Site specific studies will examine the influence of particular watersheds on the dynamics of adjacent reef communities. Regional studies will place the specific watershed effects in the context of larger regional patterns. Process oriented experimental studies to examine the impact of the terrestrial runoff are discussed below in section 4. Kelp forest community responses to terrestrial input.

#### REGIONAL SCALE STUDIES:

The extent of terrestrial influence on reef habitats throughout the Santa Barbara Channel will be characterized using satellite imagery and field surveys. The satellite studies will provide daily, synoptic, large scale (1 km and larger) views of the coastal ocean. For example, Advanced Very High Resolution Radiometer (AVHRR) imagery can be used to determine a qualitative index for seawater turbidity (Stumpf and Pennock 1989, see Figure 2). Advanced marine resource monitoring techniques are being made available from our Plumes and Blooms program (Garver and Siegel, 1997; Toole and Siegel, in progress) using data from the Sea-viewing Wide Field of View Sensor (SeaWiFS) and shortly using MODIS (to be launched in 1999). A satellite acquisition and analysis facility is located at UCSB and AVHRR imagery of sea surface temperature, water turbidity as well as SeaWiFS ocean color products (chlorophyll, suspended sediments, colored organic material concentrations and primary production) are available (<http://www.icess.ucsb.edu/avhrr>). High spatial resolution (~30 m), multispectral images are available from Landsat-7 imagery that will be used to provide periodic estimates of vegetation in the watersheds, kelp canopy coverage, and near-shore suspended sediment concentrations (e.g., Mertes et al. 1993; 1998; Deysher, 1993). In addition, we will acquire available high spectral (10 nm) and spatial (up to 30 m) imagery from the Naval Earth Map Observer (NEMO) which is scheduled for launch in August of 2000 (<http://nemo.nrl.navy.mil>). The Santa Barbara Channel is presently one of their study sites, and they will share available hyperspectral ocean color imagery with us in exchange for ground truthing data on our reef study sites (C.O. Davis, personal communication, June 21, 1999).

In addition to mapping runoff via satellite imagery, we will collect seasonal *in situ* measurements of temperature, salinity, optical measures of phytoplankton biomass and suspended sediment concentrations near the reef sites using small boats and throughout the Santa Barbara Channel using UNOLS vessels. A minibat undulating towed fish will provide synoptic surveys of the coastal zone in order to assess the spatial extent of terrestrial inputs by analyzing the 3-D structure of the resulting salinity and suspended sediment fields. The minibat towed fish surveys will be used to link spatial scales of measurements at our kelp forest sites (10's m to 1 km) to larger ocean scales (>1 km). Discrete water samples for chlorophyll analysis collected on survey cruises will provide vital ground truthing for estimates of phytoplankton biomass and productivity from both the minibat surveys and satellite imagery.

Water samples will be collected at varying distances downcoast from stream mouths and analyzed for the same constituents as water samples collected in the watershed. Larger scale estimates of nutrient concentration and elemental composition will also be measured during the survey cruises to be done several times during the wet and dry seasons. These large scale surveys will be conducted during the first three years of the project. Data collected from these surveys will be used to determine the sea surface (SST)-nutrient relationship for the Channel. Thereafter, regional scale estimates of nutrient availability will be derived by assuming a seasonally varying

SST–nutrient relationship applied to AVHRR SST imagery processed at UCSB ([www.icess.ucsb.edu/avhrr](http://www.icess.ucsb.edu/avhrr); Dugdale et al. 1997).

#### SITE SPECIFIC STUDIES:

Continuous data from moored instruments at each reef site will be used to provide a high temporal resolution record of terrestrial and oceanic influence on the kelp forest ecosystem. The instrumentation and manpower necessary for this ocean monitoring would be impossible without the collaborative support of Gaines and Warner's long term funding from the Packard Foundation. A multi-instrumented moored system (Dickey 1991, Dickey and Siegel 1993) has been installed at 15 m depth in the kelp beds located at the mouths of each watershed. An additional 10 moorings installed in the Santa Barbara Channel and north of Pt. Conception will provide a broader regional perspective. Each moored system collects data on seawater temperature and salinity, the *in situ* solar flux in the PAR band, phytoplankton biomass via chlorophyll a fluorescence, suspended sediment concentration by optical backscatter sensor, and larval abundance for a suite of invertebrate and fish species. These data will be used to determine the timing and relative magnitude of terrestrial and oceanic inputs to the kelp forest ecosystem (data on solar flux and chlorophyll fluorescence will be used in studies of primary production - see below).

Instruments that determine the dominant ocean processes that modify and disperse terrestrial inputs are also installed in each kelp bed as part of Gaines' and Warner's research program. Currents through the kelp forests are measured with acoustic Doppler current profilers (ADCP), which are bottom-deployed in an upward-looking configuration to provide profiles of horizontal velocity throughout the water column. Additional current information comes from an array of 5 high-frequency radar units (Coastal Ocean Dynamics Applications Radars, CODAR) that map hourly surface currents over a wide area of the Channel, and an array of moored current meters that are part of ongoing studies funded by the Minerals Management Service. The CODAR current fields will be combined with the ocean color products discussed above to produce estimates of transport of biogenic and other materials in and out of our reef study sites. Continuous measurements of wave height and period will be made using bottom pressure gauges. Wave direction will be obtained from buoy data and the wave model output available over the Internet (<http://cdip.ucsd.edu/models/wave.model.shtml>). Measuring waves is also important because the storms that generate runoff also produce waves, which are an important source of disturbance in shallow coastal reefs (Ebeling et al. 1985, Denny 1988, Seymour et al. 1989). The fact that terrestrial and ocean based disturbances coincide in time, may have important implications to reef community dynamics.

The transport of nutrients from land to sea also has the potential to influence terrestrial food webs (reviewed in Polis et al. 1997) because a substantial amount of kelp production is dislodged by waves and transported to the beach (Gerard 1976). Kelp wrack on the beach serves as a primary source of food for a suite of meso-invertebrate grazers, which in turn are the primary prey of shorebirds (Bradley and Bradley 1993). The data that we collect on kelp production and mortality (see below), nutrient supply and wave climate will be used by Dugan in her ongoing studies of this terrestrial food web to determine the degree to which it is influenced by marine versus terrestrial processes.

### *3. Ecosystem Dynamics in the Terrestrially Influenced Coastal Zone*

**Background:** Both macroalgae and phytoplankton contribute to primary production in kelp forests. Some evidence suggests that phytoplankton production is small relative to that of macroalgae in the kelp forest (Platt 1971), but direct measures of phytoplankton productivity within kelp forests have not been reported. Even if phytoplankton production is small relative to that of macroalgae, phytoplankton can nonetheless be a dominant food source and a potential determinant of community structure in kelp forests similar to what has been shown for the rocky intertidal (Menge et al. 1997). This is because the availability of phytoplankton in kelp forests is determined not only by the level of local production in the coastal zone, but also by the magnitude and fraction of phytoplankton production in the Channel that is advected to the kelp

forest. Both nearshore and offshore processes affecting phytoplankton production are impacted by runoff events (Figure 2).

There is strong seasonal and interannual variability in ocean productivity in the coastal waters of southern California. This variability is largely driven by variability in nutrients, mainly nitrate (Jackson 1977, Wheeler and North 1981, Gerard 1982, Zimmer and Kremer 1984). Terrestrial runoff has the potential to increase primary production in the coastal zone by increasing concentrations of nutrients above those of ambient seawater. Runoff also has the potential to decrease primary production in the coastal zone because it typically results in high levels of suspended sediments, which greatly reduce light in the kelp forest leading to a reduction in reef productivity. Production of giant kelp and other algae may be particularly susceptible to runoff effects because the period of greatest runoff and highest turbidity coincides with their peak period of spore production, dispersal, and recruitment (Reed et al. 1988, Reed 1990, Reed et al. 1997). The successful recruitment of young microscopic stages of these algae is critically dependent on conditions of high light and low sedimentation (Deysher & Dean 1986, Devinsky & Volse 1978) which are typically rare in areas of high runoff. In addition to phytoplankton, and kelp-derived detritus, terrestrially-derived POM could serve as an important food source to primary consumers in kelp forests located close to sources of freshwater runoff (Polis et al 1997).

Focal Questions: *How does primary productivity on coastal reefs vary with the magnitude and extent of terrestrial input? How do the contrasting influences of sediments and nutrients in terrestrial runoff alter processes that control primary production in coastal reef ecosystems? Does terrestrially derived POM play an important energetic role in marine food webs?*

Approach:

#### PATTERNS OF PRIMARY PRODUCTION

The modeling of macroalgal and phytoplankton primary production rates from the optical data collected on the moorings or from satellite imagery of ocean color requires that the underwater light field be determined on appropriate time and space scales. Fractional cloud coverage and incident light flux (in the PAR band) will be determined from AVHRR satellite data enabling daily mean fluxes to be determined at the ocean surface (e.g., Gautier et al. 1980; Frouin et al. 1989). The solar fluxes are then propagated to depth using models of the spectral attenuation coefficient. Light-field modeling is a focus of our on-going Plumes and Blooms study (<http://www.ices.ucsb.edu/PnB>) and will be extended into the reef habitats in this study. Values of light-field attenuation may be derived from the proposed moored optical sampling or from satellite ocean color imagery (SeaWiFS; Ohlmann et al. 1996).

We will estimate macroalgal production from bimonthly measurements of standing crop and whole plant growth. Because most species of macroalgae inhabiting kelp forests appear to show similar seasonal patterns of productivity (Breda 1982, Heine 1983, Reed 1990b) we will focus our measurements initially on the giant kelp *Macrocystis pyrifera*, which is the largest producer of biomass in the kelp forest (Foster and Schiel 1985). The standing stock of giant kelp will be estimated from aerial photographs of surface canopies (taken in collaboration with the Channel Islands Marine Sanctuary), which will be ground-truthed by diver surveys. Whole plant growth will be measured in marked individuals over time by following the loss and addition of fronds and changes in individual frond size and weight (Gerard 1976, Coon 1982).

Phytoplankton biomass at each of the three kelp forest sites will be estimated from high temporal resolution records of chlorophyll concentration using moored fluorometers with periodic calibration during minibat surveys and mooring maintenance cruises. Phytoplankton productivity will be measured at the three kelp forest study sites, and in adjacent offshore waters during the seasonal surveys. Estimates of the annual phytoplankton productivity in the kelp forest and surrounding ocean by conventional means are not practical as it requires more intensive sampling than can be sustained by the core LTER funds. Therefore the time history of phytoplankton productivity on the reefs will be determined by coupling seasonal measurements of  $^{14}\text{C}$  uptake and chlorophyll biomass to bio-optical models that can exploit the high-resolution temporal record from moored sensors and satellite imagery of ocean temperature and color (e.g., Smith et al. 1989). After algorithms for estimating phytoplankton biomass and productivity from

optical data are established, phytoplankton biomass and productivity will be estimated solely from ocean optics in future years.

#### CONTROLS ON PRIMARY PRODUCTION

Experiments will be done to evaluate the controls on primary production of macroalgae and phytoplankton at the three kelp forest sites as well as at sites on Santa Cruz Island which experience little terrestrial influence. Because increased turbidity and nutrient loading are two of the most likely ways that runoff may influence primary production, our initial investigations will focus on the effects of light and nutrients. Limitation of nitrogen use by kelp and phytoplankton will be evaluated seasonally. Kinetic experiments to examine the dependence of nitrate uptake rates on nitrate availability by phytoplankton (Eppley et al. 1969) and macroalgae (O'Brien and Wheeler 1987) will be performed using  $^{15}\text{NO}_3^-$  and analyzed using a Europa Tracer Mass spectrometer. The effect of light will be examined for both phytoplankton and macroalgae using productivity vs. irradiance models. P vs. I curves will be established for phytoplankton at each site using  $^{14}\text{C}$  bicarbonate uptake at least seasonally exploiting the sampling opportunities provided by the minibat surveys and the basin-wide surveys on UNOLS vessels. *Macrocystis* photosynthetic performance will be measured in the laboratory polarographically in temperature controlled magnetically stirred chambers that are illuminated by high intensity, broad spectrum irradiance. It is also likely that we will be able to explain a good deal of the variability in our  $P_{\text{max}}$  measurements in terms of ancillary data, such as SST or canopy coverage. These parameters may also be determined from remote sensing data, which will help us extrapolate our estimates to nearshore habitats.

#### THE USE OF STABLE ISOTOPE ANALYSES AND THE ROLE OF TERRESTRIALLY DERIVED POM

We will use stable carbon and nitrogen isotope ratio analysis of consumers of varying trophic status to evaluate the relative contribution of phytoplankton and kelp detritus to reef food webs during periods of low freshwater runoff and to identify whether terrestrially-derived POM is incorporated into reef food webs following periods of storm discharge. The use of stable isotope ratios in food web studies is well-established and the merits and limitations of the technique are reviewed in Fry and Sherr (1984), Simenstad and Wissmar (1985), and Currin et al. (1995). The dual isotope approach proposed here provides greater power in resolving differences among food sources than a single isotope approach (e.g., Peterson et al. 1985). The carbon isotope ratio (expressed as  $\delta^{13}\text{C}$  in ‰) of a consumer closely reflects the ratio of dietary carbon (DeNiro and Epstein 1978, Fry and Sherr 1984) whereas the stable nitrogen isotope ratio is typically enriched in  $^{15}\text{N}$  from 2 to 4 ‰ relative to dietary nitrogen (DeNiro and Epstein 1981, Peterson and Fry 1987).

To identify carbon and nitrogen sources used by kelp forest consumers, we will measure the isotopic composition of experimental populations of mussels (*Mytilus galloprovincialis*) and of resident reef species. Small mussels (20 mm shell-length) will be placed in vexar mesh cages and transplanted to multiple locations in each of the three kelp beds along a gradient away from the runoff source. Mussels will be obtained from sites on the Channel Islands that are subjected to minimal terrestrial runoff. To elucidate possible temporal changes in the importance of food sources to kelp forest consumers, mussels will be transplanted during periods of highest (Dec to Mar) and lowest (Jun to Sep) terrestrial runoff. Small mussels grow rapidly, increasing in shell-length from 20 to 50 mm in 4 months (Page and Hubbard 1987), providing sufficient tissue increase, and thus carbon and nitrogen turnover, to reflect local dietary sources of POM. We will also sample representative deposit-feeding (e.g., amphipods, sea cucumbers), suspension-feeding (e.g., barnacles, tunicates), and predatory (e.g., starfish, surfperch) species at each reef and intertidal site following the rainy season and during the dry season.

Phytoplankton-dominated POM has a  $\delta^{13}\text{C}$  value of approximately -21‰ (Fry and Sherr 1984, Peterson et al. 1985, Simenstad and Wissmar 1985) whereas kelp-dominated POM is enriched in  $^{13}\text{C}$  (e.g., preliminary  $\delta^{13}\text{C}$  value for *Macrocystis pyrifera* = -10.6‰, Page, unpubl. data; Duggins et al. 1989). During periods of low freshwater discharge, the divergent  $\delta^{13}\text{C}$  end-members of phytoplankton and kelp will permit an estimate of the relative use of these sources by consumers with a simple two source mixing model (Fry and Sherr 1984; Duggins et al. 1989).

If kelp forest suspension-feeding consumers use appreciable amounts of terrestrially-derived POM following periods of storm runoff, we predict that this will be reflected in a gradient of depleted  $\delta^{13}\text{C}$  signatures of experimental mussels towards the source of freshwater.  $^{13}\text{C}$ -enrichment of suspension-feeders often occurs along a gradient with increasing distance from riverine sources of  $^{13}\text{C}$ -depleted POM (e.g., Incze et al. 1982, Stephenson and Lyon 1982, Riera and Richard 1996). Specimens for isotopic analysis will be processed using standard techniques (e.g., Currin et al. 1995; Page in press) and the natural abundance of carbon and nitrogen isotopes determined by isotope mass spectrometry in the Marine Science Institute Analytical Laboratory.

#### *4. Kelp Forest Community Responses to Terrestrial Input*

**Background:** Given the unique trophic structure of reef communities (Fig 4), processes that alter the relative strengths of the linkages in the food web may greatly alter the composition of the community. For example, changes in the abundance of phytoplankton and/or dissolved nutrients available to kelp could shift these communities from dominance by benthic macroalgae to sessile invertebrates and vice versa (Menge et al. 1997). Similarly, variation in offshore production by phytoplankton could affect the invertebrate dominance of reefs by controlling the successful development of planktonic larvae. If settlement rates of invertebrates vary with changes in production of phytoplankton, then population dynamics and species dominance on the reef could be controlled by the processes that regulate local and regional patterns of primary production (see above). Dramatic shifts between the relative abundance of filter feeders and macroalgae have been observed several times in the last 20 years (Richards et al. 1997, Schmitt and Holbrook, unpubl data), however the causes for such changes in community structure remain speculative. One possible hypothesis is that the shifts in community dominance from algae to invertebrates and vice versa are responses to temporal variation in nutrient availability.

Additional complexities in the trophic structure of kelp forests stems from the existence of two major pathways within the macroalgal foodweb. The most recognized path involves the direct consumption of macroalgae by large herbivores (e.g. sea urchins and gastropods) which in turn are preyed upon by large predators (e.g. sea otters). Sea urchins are well known for causing the loss of nearly all macroalgae in kelp forests world wide, and intense grazing by them can have cascading effects on secondary and tertiary consumers (reviewed in Dayton 1985, Harrold and Pearse 1987). Such intense grazing by sea urchins does not occur in areas inhabited by sea otters where lush kelp forests are the norm (Van Blaricom and Estes 1988). Sea otters were extirpated from southern California over one hundred years ago (reviewed in Kenyon 1969) and kelp forests in the LTER site show frequent transitions between densely vegetated and barren states (Ebeling et al. 1985, Harrold and Reed 1985). In the last several years, however, sea otters have begun recolonizing kelp forests along the coast of Santa Barbara and a LTER site in this region would provide an ideal opportunity to investigate changes in trophic structure over an appropriate time scale. A less publicized, but equally important pathway involving macroalgae entails periphyton growth on foliose algae. Periphyton is grazed by meso-invertebrates (e.g., amphipods) taking refuge in the algae, which in turn are the primary food source of demersal fishes in the kelp forest.

The relative contributions of bottom-up vs. top-down control for these two macroalgal pathways have not been quantified. Although there has been considerable work regarding the effects of sea otters on interactions among sea urchins, kelp and foliose algae, little is known regarding bottom-up effects for this set of interacting species. In contrast, no evidence is available to assess whether fish limit the abundances of meso-invertebrate grazers, or if so, whether this results in increased abundances of the periphyton. Some evidence exists for this food web that suggests bottom-up control is strong. Our time series sampling of kelp forests at Santa Cruz Island, in the proposed LTER site, since 1982 provides some of the most compelling evidence that declines in abundances of species in upper trophic levels probably resulted from falling productivity at the lowest level (i.e., 'bottom-up' forcing). Abundances of surfperches - sedentary reef fishes that feed on benthic meso-invertebrates and give birth to non-dispersing young - fell by ~80% between 1982 and 1995, which mirrored falling abundances of most other

co-occurring reef fishes (21 of 22 species declined by an average of ~70%; Holbrook *et al.* 1997). During this period, productivity of the surfperch food supply declined by ~ an order of magnitude, and the decrease in surfperch abundance resulted largely from a decline in the production of newborns in a manner that mirrored annual change in the adult food supply. Indeed, annual year-class strength of newborn surfperches was tightly coupled with annual productivity of the adult food supply on the reefs ( $r^2 = 0.90$ ;  $P < 0.001$ ; Holbrook *et al.* 1997). Our sampling also indicated that standing stocks of benthic primary producers and of meso-invertebrate grazers also fell by ~80% during this period (Holbrook and Schmitt 1996, Holbrook *et al.* 1997). The pattern of observed proportionate declines in all trophic levels of the benthic community at the proposed LTER site suggest that two models of regulation that have been applied to marine communities do not depict this system. In particular, effects of reduced nutrient supply were neither expressed at alternating trophic levels as predicted by the HHS model (e.g., Hairston *et al.* 1960, Fretwell 1977, Oksanen 1988; Power 1990), nor was the effect size the smallest for the top trophic level as predicted by the Menge and Sutherland model (Menge and Sutherland 1976, 1987). Long-term nutrient addition experiments done over a range of oceanographic and climatic conditions would provide much needed insight into the mechanisms that regulate these trophic interactions and the degree to which they are influenced by nutrients of terrestrial origin.

Focal Questions: *Do demographic and population characteristics of kelp forest species vary with the degree of terrestrial inputs? How do changes in nutrient supply influence trophic interactions? Will terrestrial influences on coastal reefs change in response to recolonization by sea otters?*

Approach:

#### LONG-TERM MONITORING OF DEMOGRAPHIC AND POPULATION PARAMETERS

The abundance, size structure and various demographic parameters (e.g., recruitment, growth, reproduction, and mortality) of key species are currently being monitored in permanently marked areas at our three kelp forest sites as part of Gaines and Warner's long-term investigations. Data are being collected seasonally on species that represent the major trophic levels depicted in Figure 4, including macroalgae (kelps and understory), sessile particle feeders (e.g., mussels and barnacles), grazers (e.g., sea urchins and snails), 1<sup>o</sup> predators (seastars, whelks), and 2<sup>o</sup> predators (fish) using sampling protocols that are compatible with the National Park Service's long-term kelp forest monitoring program at the Channel Islands. Infrared photographs taken from aerial overflights by the Channel Islands National Marine Sanctuary will be done semi-annually in the winter and summer to measure regional changes in the area of kelp canopy throughout the LTER site. Data from these other monitoring programs combined with satellite imagery data will be used to evaluate the extent to which regional changes in population dynamics and community structure are related to the degree of terrestrial influence.

#### THE INFLUENCE OF CHANGES IN NUTRIENT SUPPLY ON TROPHIC INTERACTIONS.

We will use short and long-term experiments and modeling to investigate the extent to which trophic interactions in the various food webs of the kelp forest ecosystem are influenced by an elevated supply of nutrients. Although we will examine the relative contributions of nutrients and top-down control for both macroalgal pathways over the course of the LTER program, we initially will focus on the much less studied periphyton--mesograzers-reef fish foodweb. We plan a series of short- and long-term field experiments to quantify the separate and joint responses of the community to nutrient supply and top-down control. Long-term experiments are necessary to measure the numerical response of the top trophic level (reef fishes) to nutrient manipulation, and to distinguish between short and longer-term changes in the primary producer assemblage. Although the responses of many species of reef fishes will be quantified, we will emphasize fishes in the family Embiotocidae (surfperches) because (1) they are among the numerically dominant consumers of meso-invertebrates on these reefs, (2) much is known regarding their foraging biology, population dynamics (and regulation), interspecies interactions and responses to establishment of giant kelp at the LTER site (Hixon 1990, Holbrook & Schmitt 1984, 1986, 1988a,b, 1989, 1992, 1995, Holbrook *et al.* 1990, Schmitt & Holbrook 1984 a,b, 1985, 1986,

1990a,b), and (3) we have a 17 year time-series of information on (a) the abundance of adults, juveniles and young-of-year, (b) densities of their prey items (meso-invertebrates), and (c) the cover and biomass of benthic algae and other substrata at Santa Cruz Island. Finally, unlike most reef fishes with demographically open populations, surfperches give birth to fully developed juveniles that do not disperse from the parental population (Schmitt & Holbrook 1990a). This life history feature will enable us to tie unambiguously possible numerical responses of these fishes to our manipulations.

The field experiments will involve orthogonal manipulations of nutrients and top predators (fishes) at sites on Santa Cruz Island that are exposed to minimal runoff and are well away from the major influence of mainland watersheds. Our nutrient addition experiments at island sites will be designed to mimic mainland reefs exposed to nutrient-laden runoff from LTER watersheds. Several responses by the assemblage of benthic primary producers to nutrient addition may occur, which could reflect variation in the temporal scale of response to the manipulation. If nutrient addition enhances the productivity of periphyton, it is likely to do so very soon after the manipulation begins; the extent to which this translates into greater periphyton standing stock will depend on the response of the meso-invertebrates, and in turn, the degree to which populations of these grazers are controlled by reef fishes. On a somewhat longer time scale, the biomass of foliose algae may increase (perhaps accompanied by a shift in the relative abundance of species within this group), which would provide more substrata for both periphyton and meso-invertebrates. Finally, over a longer time-scale, giant kelp could become established and develop into dense forests that reduce light levels reaching understory algae (Reed and Foster 1984). This can reduce productivity of periphyton and biomass of foliose algae (Schmitt and Holbrook 1990b). In addition to bottom-up control, the effects of top predators will be examined by excluding them from certain reef areas (half of which receive enhanced nutrients), and biomass responses of both the meso-invertebrate and periphyton will be quantified. This experiment will enable us to quantify the relative contributions of bottom-up and down-top control, will reveal long-term community responses to differences in nutrient regimes, and will provide data needed to refine our models of community regulation.

Similar nutrient addition experiments at our Santa Cruz island sites will be done to test whether macroalgae and sessile suspension feeders compete for nutrients. Here replicate 1 m x 2 m plots will be established in areas dominated by macroalgae and in areas dominated by sessile filter feeders. Half of the plots will be randomly selected and exposed to time release fertilizers to determine whether nutrients alone can invoke a shift in species composition. Furthermore, half of each plot will be cleared to bare rock to test whether a disturbance is needed to initiate a change in species composition. Experiments will be maintained and monitored over the long-term to determine the degree to which nutrient competition between macroalgae and filter feeders is influenced by changes in oceanographic conditions.

The ultimate goal of the reef modeling is to construct a suite of models of the three interconnected food webs that allow us to make predictions about the long-term dynamics of the community, especially in response to changing oceanographic regimes or sea otter recolonization. The complexity of any full model will make it somewhat intractable however, so we will begin with submodels that target particular food chains or pairwise interactions between species in different trophic chains. In these submodels, resources such as nutrients, light, and space will be treated explicitly as environmental variables.

Our initial modeling effort will focus on the periphyton-mesograzer-reef fish food web, using formalism previously developed at UCSB (Nisbet et al. 1997). We will use the existing extensive data on this system to build and parameterize a dynamic model that can explain the community response to the 1976-77 oceanographic regime shift (Fig 5). Many of the processes (e.g. functional response of fish) will be determined directly from experimental data. For the surfperch in particular we have extensive demographic data that allow us to examine issues such as density dependence, which may explain the mismatch between simple models and the community's response to nutrient change. Other processes may only be known qualitatively (e.g., amphipod grazing). Rather than assuming arbitrary functional forms for these, we will use flexible forms such as splines and then fit the models to the time series data using "inverse methods" (Wood

1999, Ellner et al. 1998, Kendall et al. 1999). This allows us to uncover functional forms that are most consistent with the observed dynamic patterns. We will use this parameterized model to make predictions about the outcomes of the nutrient-manipulation experiments. We will also use it to guide the magnitude and timing, for pulsed perturbations, of the nutrient addition.

Our second modeling focus will be on competition for space between kelp and sessile filter feeders. We will model settlement, juvenile survival, and adult fecundity as a function of the environmental variables (nutrients, turbidity, sediments) associated with being near or far from terrestrial inputs. The timing and pulsed nature of both terrestrial and oceanic nutrient inputs will be explicitly included in the model. We will also examine intra- and interspecific interactions: pre-emptive space use, and light competition (models suggest that mature kelp forest may suppress juvenile kelp to such an extent that there may be generation-long cycles in recruitment – Nisbet and Bence 1989). This model will make predictions about the effects of the nutrient and disturbance manipulations on the relative abundance of kelp and filter feeders. We will contrast these predictions with those made by a model that includes adjacent trophic levels (phytoplankton, urchins) to determine the importance of the trophic structure on the predictions of models of space competition. The latter model will include detailed resource uptake and growth models for phytoplankton and kelp, to predict how individuals will respond to particular patterns of nutrients and sediments. Of particular interest will be the magnitude and timing of nutrient storage (e.g., Fong et al. 1994), and whether the different autotrophs respond differently to the differing N:P ratios from oceanic and terrestrial inputs (Elser and Urabe 1999).

#### **RELATIONSHIP OF PROPOSED WORK TO INTER-LTER SITE RESEARCH ACTIVITIES.**

The proposed LTER will make strong contributions to a number of major themes that are becoming important throughout the LTER Network. These include: terrestrial-freshwater interactions and factors that control stream processes; land-coastal ocean interactions; human impacts/urbanization effects on ecosystems; the role of climatic variability in driving ecosystem function; and the effects of spatial heterogeneity in physiochemical conditions on ecosystem processes. An LTER in the Santa Barbara area would make a unique contribution to network activities in these areas. Coastal southern California incorporates both a number of ecosystem types and a climate regime that are not represented in the LTER network. A number of sites have had a focus on terrestrial-freshwater linkages, but other than McMurdo (which is a special case), none of them are in arid or semi-arid areas (e.g. Andrews, Arctic, Baltimore, Coweeta, Hubbard Brook, Plum River). Only two sites are studying terrestrial-marine interactions, and both are on the east coast in the temperate climate region. On top of these issues, a Santa Barbara LTER would contribute greatly to studies looking at development/urbanization issues. Baltimore and Phoenix are targeted at this issue, but the Santa Barbara site would make this aspect of the network transcontinental. In areas of variability, both temporal and spatial, a Santa Barbara site would also add a dimension to the LTER network. We have a strong program for analyzing both terrestrial landscape and marine heterogeneity using remote sensing of land use patterns, ocean temperature, ocean color. Through the proposed GIS model of the area we will define variability on spatial scales from kilometers to tens of kilometers. We are also in a strong position to contribute to the analysis of the effects of El Niño/La Nina effects across the LTER network. A number of sites are already working in this area (Sevilleta, Niwot Ridge, Andrews, Konza Prairie, and North Temperate Lakes WI) and would benefit from a coastal/marine component. The geological record of the basin reveals that the signals of climatic change are stronger in the Santa Barbara Basin compared to any other region along the Pacific coast of the United States (Kennett, unpublished) making it an ideal location for detecting and evaluating climatic effects on ecosystem structure and function. The extremes of rainfall and ocean currents directly affect major interactions between terrestrial and marine influences on coastal ecosystems. That linkage provides the ability to specifically address the effects of decadal climatic fluctuations on the coastal reef ecosystem.

### Section 3 References

1. Addison, R. F. 1989. Organochlorines and marine mammal reproduction. *Canadian Journal of Fisheries and Aquatic Sciences* 46:360-368
2. Ambrose, R.F., D.C. Reed, J.M. Engle, and M.F. Caswell. 1989. California comprehensive offshore resource study: summary of biological resources. Report to California State Lands Commission.
3. Anbeek, C. 1993. The effect of natural weathering on dissolution rates. *Geochimica et Cosmochimica Acta*,57: 4963-4975
4. Andersen, D. W., J. R. Jehl, R. W. Risebrough, L. A. Woods, L. R. Deweese, W. G. Edgecomb. 1975. Brown pelicans: Improved reproduction off the southern California coast. *Science* 190:806-808.
5. Baumgartner, T. R. , A. Soutar, and V. Ferreria-Bartrina. 1992. Reconstruction of the history of Pacific Sardine and Northern Anchovy populations over the past two millenia from sediments in the Santa Barbara Basin. *CalCOFI Report* 33:24-40.
6. Behl, R.J., and Kennett, J.P., 1996, Brief interstadial events in the Santa Barbara Basin, NE Pacific, during the past 60 kyr: *Nature*, v. 379, p. 243-246.
7. Bertness, M. D., S. D. Gaines, and S. M. Yeh. 1997. Making mountains out of barnacles: the dynamics of hummock formation. *Ecology*.
8. Bertness, M., S. D. Gaines, and R. Wahle. 1996. Wind-driven settlement patterns in the acorn barnacle, *Semibalanus balanoides*. *Marine Ecology Progress Series*. 137:103-110.
9. Black. R. 1974. some biological interactions affecting intertidal populations of the kelp *Egregia laevigatz*. *Marine Biology* 28:189-198.
10. Bradley, P.M., P.B. McMahon and F.H. Chapelle. Effects of carbon and nitrate on denitrification in bottom sediments of an effluent-dominated river. *Water Resour. Res.* 31: 1063-1068.
11. Bradley, R. A. and D. W. Bradley. 1993. Wintering shorebirds increase after kelp (*Macrocystis*) recovery. *Condor* 95:372-376.
12. Bray, N.A., A. Keyes, and W.M.L. Morawitz. 1997. The California Current System in the Southern California Bight, and its influence on Circulation in the Santa Barbara Channel, submitted *J. Geophys. Res.*
13. Briggs, J. C. 1974. *Marine zoogeography*. McGraw-Hill, New York.
14. Brink, K.H., and R.D. Muench. 1986. Circulation in the Pt. Conception-Santa Barbara Channel Region, *J. Geophys. Res.*, 91: 877-895.
15. Brink, K.H., and T.J. Cowles. 1991. The Coastal Transition Zone Program. *J. Geophys. Res.*, 96: 14,637-14,648.
16. Brzezinski, M. A. and D. M. Nelson 1996. Chronic substrate limitation of silicic acid uptake rates in the western Sargasso Sea. *Deep Sea Research II* 43:437-453.
17. Brzezinski, M., D.C. Reed, and C.D. Amsler. 1993. Neutral lipids as major storage products in zoospores of the giant kelp, *Macrocystis pyrifera*. *J. Phycology* 29:16-23.
18. Brzezinski, M.A., Villareal, T.A, and Lipschultz, F. 1998. Silica production and the contribution of diatoms to new and primary production in the central North Pacific. *Mar. Ecol. Prog. Ser.* 167, 89-104.
19. Chesterikoff, A, B. Garban, G. Billen and M. Poulin. 1992. Inorganic nitrogen dynamics in the River Seine downstream from Paris (France). *Biogeochemistry* 17: 147-164
20. Clein, J. and J.P. Schimel. 1994. Reduction in microbial activity in birch litter due to drying and rewetting events. *Soil Biology & Biochemistry*. 26: 403-406.
21. Clein, J.S. and J.P. Schimel. 1995. Microbial activity of tundra and taiga soils at sub-zero temperatures. *Soil Biol. Biochem.* 27: 1231-1234.
22. Clein, J.S. and J.P. Schimel. 1995. Nitrogen turnover and availability during succession from alder to poplar in Alaskan taiga forests. *Soil Biol. Biochem.* 27: 742-752.
23. Coon, D. A. 1982. Studies of whole plant growth in *Macrocystis pyrifera*. *Botanica Marina* 24:19-27.

24. Cooper, S. D. 1988. The responses of aquatic insects and tadpoles to trout. Verh. Internat. Verein. Limnol. 23: 1698-1703.
25. Cooper, S. D., and T. L. Dudley. 1988. The interpretation of "controlled" and "natural" experiments in streams. Oikos 52:357-361.
26. Cooper, S. D., T. L. Dudley, and N. Hemphill. 1986. The biology of chaparral streams in Southern California. In: J. DeVries (ed.), Proceedings of the Chaparral Ecosystem Research Conference. Calif. Water Res. Center Contributions. Report No. 62:139-151.
27. Cooper, S.D., L. Barmuta, O. Sarnelle, K. Kratz, and S. Diehl. 1997. Quantifying spatial heterogeneity in streams. Journal of the North American Benthological Society 16: 174 - 188.
28. Cooper, S.D., S. Diehl, K. Kratz, and O. Sarnelle. 1998. Implications of scale for patterns and processes in stream ecology. Australian Journal of Ecology 23: 27-40.
29. Coury, D.A, Brzezinski, MA, Polne-Fuller, M, and Gibor, A. 1995. Analysis of viability and cell types of macroalgal protoplasts using flow cytometry. J. Appl. Phycol. 7:413-420.
30. Coury, D.A. 1993. Studies on protoplasts from commercially-important seaweeds: I. Isolation of protoplasts from the agarophyte *Gelidium robustum* (Rhodophyta). II. Analysis of macroalgal protoplasts using flow cytometry. MA Thesis, University of California, Santa Barbara. 81 pp.
31. Currin, C. A., S. Y. Newell, & H. W. Paerl. 1995. The role of standing dead *Spartina alterniflora* and benthic microalgae in salt marsh food webs: considerations based on multiple stable isotope analysis. Marine Ecology Progress Series 121: 99-116.
32. Darwin, C. 1860. The voyage of the Beagle. Reprinted in 1962. Anchor Books, Doubleday and Co., Garden City, New York.
33. Davidson, E.A. and J.P. Schimel. 1995. Microbial processes of production and consumption of nitric oxide, nitrous oxide, and methane. In: *Methods in Ecology: Trace Gases*. P. Matson and R. Harriss (Eds.). Blackwell Scientific. pp. 327-357.
34. Dayton, P. K. and M. J. Tegner. 1989. Bottoms beneath troubled waters: benthic impacts of the 1982-1984 El Niño in the temperate zone. Pages 433-72, in P. W. Glynn, editor. Global ecological consequences of the 1982-83 El Niño-Southern Oscillation. Elsevier Oceanography Series No. 52, Amsterdam.
35. Dayton, P.K. 1985. Ecology of kelp communities. Annual Review of Ecology and Systematics 16:215-246.
36. De Long, R. L., W. G. Gilmartin, and J. G. Simpson. 1973. Premature births in California sea lions: Association with organochlorine pollutant residue levels. Science 181: 1168-1170.
37. De Niro, M. J. & S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta 42: 495-506.
38. De Niro, M. J. & S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochimica et Cosmochimica Acta 45: 341-351.
39. de Roos, A.M., McCauley, E., Nisbet, R.M., Gurney, W.S.C., Murdoch, W.W. 1998. "What individual life histories can (and cannot) tell about population dynamics. Aquatic Ecology, 31: 37-45.
40. Denny, M. W. 1988. Biology and the mechanics of the wave-swept environment. Princeton University Press, Princeton, N.J.
41. Denny, M. W. and S. D. Gaines. 1999. *Chance in Biology*. Princeton University Press.
42. Devlinny, J. S. and L. A. Volse. 1978. Effects of sediments on the development of *Macrocystis pyrifera* gametophytes. Marine Biology 48:343-348.
43. Deysher LE., 1993: Evaluation of remote sensing techniques for monitoring giant kelp populations. Hydrobiologia, 261, 307-312.
44. Deysher, L. E. and T. A. Dean. 1986. In situ recruitment of sporophytes of the giant kelp *Macrocystis pyrifera*: effects of physical factors. J. Exp.Mar. Biol. Ecol. 103:41-63.
45. Dickey, T.D., 1991: The emergence of concurrent high-resolution physical and bio-optical measurements in the upper ocean and their application. Reviews of Geophysics, 29, 383-413.
46. Dickey, T.D., and D.A. Siegel, (eds.), 1993: Bio-optics in U.S. JGOFS. U. S. JGOFS Planning Report 18, Woods Hole, MA, p 180.

47. Diehl, S., S. D. Cooper, K. Kratz, R. M. Nisbet, S. K. Roll, S. W. Wiseman, and T. M. Jenkins, Jr. Effects of multiple, predator-induced behaviors on short-term producer-grazer dynamics in open systems. *American Naturalist* (in review)
48. Donalson, D.D. and Nisbet, R.M. Population dynamics and spatial scale: effects of system size on population persistence. *Ecology*, in press.
49. Douglas, P.L., G.E. Forrester and S.D. Cooper. 1994. Effects of trout on the diel periodicity of drifting in baetid mayflies. *Oecologia* 98:48-56.
50. Douros, W.J. 1993. Prehistoric predation on black abalone by Chumash Indians and sea otters. Pp. 557-566 in: F.G. Hochberg (ed.), *Third California Islands Symposium. Recent Advances in Research on the California Islands*. Santa Barbara Museum of Natural History, Santa Barbara, CA.
51. Duce, R. A., P. S. Liss, J. T. Merrill, E. L. Atlas, P. Buat-Menard, B. B. Hicks, J. M. Miller, J. M. Prospero, R. Arimoto, T. M. Church, W. Ellis, J. N. Galloway, L. Hansen, T. D. Jickells, A. H. Knap, K. H. Reinhardt, B. Schneider, A. Soudine, J. J. Tokos, S. Tsunogai, R. Wollast and M. Zhou. 1991. The atmospheric input of trace species to the world ocean. *Global Biogeochemical Cycles*. 5: 193-259.
52. Dudley, T.L. and C.M. D'Antonio. 1991. The effects of substrate texture, grazing and disturbance on macroalgal establishment in stream riffles. *Ecology* 72:297-309.
53. Dugdale, RC; Davis, CO; Wilkerson, FP. 1997. Assessment of new production at the upwelling center at Point Conception, California, using nitrate estimated from remotely sensed sea surface temperature. *Journal of Geophysical Research-Oceans* 102:8573-8585.
54. Duggins, D. O., C. A. Simenstad, & J. A. Estes. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science* 245: 170-173.
55. Ebeling, A. W. and R. N. Bray. 1976. Day vs. night activity of reef fishes in a kelp forest off Santa Barbara California. *Fishery Bulletin* 74:703-717.
56. Ebeling, A. W., D. R. Laur, and R. J. Rowley. 1985. Severe storm disturbances and the reversal of community structure in a southern California kelp forest. *Marine Biology* 84:287-294.
57. Ekman, S. 1953. *Zoogeography of the Sea*. Sedgwick and Jackson, London.
58. Ellner SP, Bailey BA, Bobashev GV, Gallant AR, Grenfell BT, Nychka DW (1998). Noise and nonlinearity in measles epidemics: Combining mechanistic and statistical approaches to population modeling. *American Naturalist* 151: 425-440.
59. Elser, J.J. and J. Urabe 1999. The stoichiometry of consumer-driven nutrient recycling: theory observations and consequences. *Ecology* 80: 735-751.
60. Englund, G., O. Sarnelle, and S.D. Cooper. 1999. The importance of data selection criteria: meta-analyses of stream predation experiments. *Ecology* 80: 1132-1141
61. Epply, R. W., J. N. Rogers and J. J. McCarthy. 1969. Half-saturation constants for uptake of nitrate and ammonium by marine phytoplankton. *Limnology and Oceanography* 14:912-920.
62. Fan, T. W.-M., R. M. Higashi, G. N. Cherr, and M. C. Pillai. 1992. Use of noninvasive NMR spectroscopy and imaging for assessing produced water effects on mussel reproduction. *in* "Produced Water" J. P. Ray and F. R. Engelhardt, editors, Plenum Press, New York. pp.403-414.
63. Ferren, W.R., Jr., Capelli, M.H., Parikh, A., and others, 1990, *Botanical Resources at Emma Wood State Beach and the Ventura River Estuary, California: Inventory and Management: The Herbarium-Department of Biological Sciences Environmental Report #15*.
64. Fisher, S.G. N.B. Grimm, E. Marti, R.M. Holmes, and J.B. Jones. 1998. Material spiraling in stream corridors: A telescoping ecosystem model. *Ecosystems*. 1: 19-34.
65. Fitzwater, S. E., G. a. Knaur and J. H. Martin. 1982. Metal contamination and its effects on primary production measurements. *Limnology and Oceanography* 27:544-551.
66. Fong, P., T.C. Foin, and J.B. Zedler. 1994. A simulation model of lagoon algae based on nitrogen competition and internal storage. *Ecological Monographs* 64:225-247.
67. Foster, M. S. 1975a. Algal succession in a *Macrocystis pyrifera* forest. *Marine Biology* 32:313-329.

68. Foster, M. S. 1975b. Regulation of algal community development in a *Macrocystis pyrifera* forest. *Marine Biology* 32:331-342.
69. Foster, M.S and D. R. Schiel 1985. The ecology of giant kelp forests in California:a community profile. U.S. Fish Wildl. Serv. Biol. Rep. 85(7.2) 152 pp.
70. Fraser, R H, P. K. Barten, and D. A. K. Pinney. 1998. Predicting stream pathogen loading from livestock using a geographical information system-based delivery model. *Journal of Environmental Quality*: 935-945.
71. Fretwell, S.D. 1977. The regulation of plant communities by food chains exploiting them. *Perspectives in Biology and Medicine* 20:169-185.
72. Frouin R; D. W. Lingner, C. Gautier; K. S. Baker; and others.1989. A simple analytical formula to compute clear sky total and photosynthetically available solar irradiance at the ocean surface. *Journal of Geophysical Research-Oceans*, 94:9731-9742
73. Fry, B. & E. B. Sherr. 1984.  $d^{13}C$  measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contributions in Marine Science* 27: 13-47.
74. Gabric, A.J. and P.R.F. Bell. 1993. Review of the effects of non-point nutrient loading on coastal ecosystems. *Aust. J. Mar. Freshwat. Res.* 44: 261-283.
75. Gaines, S. D. 1997. Biogeographic boundaries and species distribution. *Alolky* 10:10.
76. Gaines, S. D. and K. Lafferty. 1995. Modeling the dynamics of marine species: the importance of incorporating larval dispersal. in *Ecology of Marine Invertebrate Larvae*, Larry McEdward ed. CRC Press. pp 389-412.
77. Gaines, S. D. and M. Bertness. 1994. Does variable transport generate variable settlement in coastal and estuarine species? in Changes in Fluxes in Estuaries, K. Dyer & R. Orth (eds.). Olsen and Olsen, London. 315-322.
78. Garver, S.A., and D.A. Siegel, 1997a. Inherent optical property inversion of remote sensing reflectance and its biogeochemical interpretation. In press, *Journal of Geophysical Research*.
79. Garver, S.A., and D.A. Siegel, 1997b. Global assessment of an inherent optical property inversion model. In press, SeaWiFS Tech. Memo. Series as part of the SeaBAM workshop report. (also available at <http://www.icess.ucsb.edu/~garver/seabam.html>)
80. Gautier, C, G.R Diak and S Masse, 1980, A simple physical model to estimate solar radiation at the sea surface from GOES satellite data. *J Appl Met*, 19:1005-1012
81. Gerard, V. A. 1976. Some aspects of material dynamics and energy flow in a kelp forest in Monterey Bay, California. Dissertation, Univ. California Santa Cruz.
82. Gerard, V. A. 1982. In situ rates of nitrate uptake by giant kelp *Macrocystis pyrifera*, tissue differences, environmental effects and predictions of nitrogen limited growth. *J. Exp. Marine Biol. Ecol.* 62:211-224.
83. Gilliom, R.J. and others. 1999. Testing water quality for pesticide pollution. *Environ. Sci. Tech.* 44: 164-169.
84. Gullledge J. and J.P. Schimel. Controls over carbon dioxide and methane fluxes across a taiga forest landscape. *Ecosystems*. In review.
85. Gullledge, J. and J.P. Schimel. 1998. Low-concentration kinetics of atmospheric  $CH_4$  oxidation in soil and the mechanism of  $NH_4^+$  inhibition. *Applied and Environmental Microbiology*. 64: 4291-4298.
86. Gullledge, J. and J.P. Schimel. 1998. Moisture Control over Atmospheric  $CH_4$  Consumption and  $CO_2$  Production in Physically Diverse Soils. *Soil Biol. Biochem.* 30: 1127-1132.
87. Gullledge, J.M., A.P. Doyle, and J.P. Schimel. 1997. Different  $NH_4^+$ -Inhibition patterns of soil  $CH_4$  consumption: a result of distinct  $CH_4$  oxidizer populations across sites? *Soil Biology and Biochemistry*. 29: 13-21.
88. Gullledge, J.M., P.A. Steudler, and J.P. Schimel. 1998. Effect of  $CH_4$ -starvation on atmospheric  $CH_4$  oxidizers taiga and temperate forest soils. *Soil Biology Biochemistry*. 30:1463-1467.
89. Gurney, W.S.C. and Nisbet, R.M. (1998). *Ecological Dynamics*. Oxford Universty Press, New York.

90. Gurney, W.S.C., Middleton, D.A.J., Nisbet, R.M., McCauley, E., Murdoch, W.W. and DeRoos, A.M. 1996. Individual energetics and the equilibrium demography of structured populations. *Theor. Pop. Biol.*,49: 344-368.
91. Gurney, W.S.C., Middleton, D.A.J., Ross, A.H., Nisbet, R.M., McCauley, E., Murdoch, W.W. and DeRoos, A.M. 1995. Modelling techniques and data requirements in aquatic systems management. *In Aquatic Predators and their Prey* (S. Greenstreet, Ed.). pp 86-97. Blackwells, Oxford, UK.
92. Hacker, S. and S. D. Gaines. 1997. Some implications of direct positive interactions for community species diversity. *Ecology*. 78:1990-2003.
93. Hairston, N.G., F.E. Smith and L.B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* 61: 817-826.
94. Harrold, C. and D. C. Reed. 1985. Food availability, sea urchin grazing and kelp forest community structure. *Ecology*. 63:547-560.
95. Harrold, C. and J. S. Pearse. 1987. The ecological role of echinoderms in kelp forests. Pages 137-233 *In* M. Jangoux and J.M. Lawrence, editors, *Echinoderm studies*. A.A. Balkema, Brookfield.
96. Heine, J. N. 1983. Seasonal productivity of two red algae in a central California kelp forest. *J. Phycology* 19:146-152.
97. Hemphill, N. , and S. D. Cooper. 1983. The effect of physical disturbance on the relative abundances of two filter-feeding insects in a small stream. *Oecologia* 58:378-382.
98. Hemphill, N., and S. D. Cooper. 1984. Differences in the community structure of stream pools containing or lacking trout. *Verh. Internat. Verein. Limnol.* 22:1858-1861.
99. Henderschott, M.C., and C.D. Winant. 1996. Surface circulation in the Santa Barbara Channel. *Oceanography*, 9, 2: 114-121.
100. Hickey, B.M. 1979. The California Current System - Hypotheses and facts. *Prog. In Oceanogr.* 8: 191-279.
101. Hixon, M.A. 1990. Competitive interactions between California reef fishes of the genus *Embiotoca*. *Ecology* 61: 918-931.
102. Hogan, J. W. and J. L. Brauhn. 1975. Abnormal rainbow trout fry from eggs containing high residues of PCB (Aroclor 1242). *Prog. Fish Cult.* 37:229-230.
103. Holbrook, S.J. 1993. The effects of food density and dispersion on patch selection by foraging black surfperch. Pp. 485-493 in: F.G. Hochberg (ed.), *Third California Islands Symposium. Recent Advances in Research on the California Islands*. Santa Barbara Museum of Natural History, Santa Barbara, CA.
104. Holbrook, S.J. and R.J. Schmitt. 1984. Experimental analyses of patch selection by foraging black surfperch (*Embiotoca jacksoni* Agassiz). *Journal of Experimental Marine Biology and Ecology* 79:39-64.
105. Holbrook, S.J. and R.J. Schmitt. 1986. Food acquisition by competing surfperch on a patchy environmental gradient. *Environmental Biology of Fish* 16: 135-146.
106. Holbrook, S.J. and R.J. Schmitt. 1988a. The combined effects of predation risk and food reward on patch selection. *Ecology* 69: 125-134.
107. Holbrook, S.J. and R.J. Schmitt. 1988b. Effects of predation risk on forager behavior: mechanisms altering patch choice. *Journal of Experimental Marine Biology and Ecology* 121: 151-163.
108. Holbrook, S.J. and R.J. Schmitt. 1989. Resource overlap, prey dynamics and the strength of interspecific competition. *Ecology* 70: 1943-1953.
109. Holbrook, S.J. and R.J. Schmitt. 1992. Causes and consequences of dietary specialization in surfperch: patch choice and intraspecific competition. *Ecology* 73: 402-412.
110. Holbrook, S.J. and R.J. Schmitt. 1995. Compensation in resource use by foragers released from interspecific competition. *Journal of Experimental Marine Biology and Ecology* 185:219-233.
111. Holbrook, S.J. and R.J. Schmitt. 1996. On the dynamics and structure of reef fish communities: are resources tracked? pp. 9-48 *In*: M.L. Cody and J.A. Smallwood (eds.) *Long-term Studies of Vertebrate Communities*. Academic Press, Inc.

112. Holbrook, S.J. and R.J. Schmitt. 1997. Settlement patterns and process in a coral reef damselfish: *in situ* nocturnal observations using infrared video. Proceedings of the VIIIth International Coral Reef Symposium 2:1143-1148.
113. Holbrook, S.J. and R.J. Schmitt. 1998. Have field experiments aided in the understanding of abundance and dynamics of reef fishes? Pp.152-169 In: W.J. Reserits and J. Bernado (eds.) Experimental Ecology: Issues and Perspectives. Oxford University Press.
114. Holbrook, S.J. and R.J. Schmitt. 1999. *In situ* nocturnal observations of reef fishes using infrared video. In: Proc. 5th Indo-Pac. Fish Conf., Nouméa, 1997 (Séret B. & J.-Y. Sire, eds), pp. 805-812. Paris: Soc. Fr. Ichtyol.
115. Holbrook, S.J. and R.J. Schmitt. 1992. Causes and consequences of dietary specialization in surfperch: patch choice and intraspecific competition. Ecology 73: 402-412.
116. Holbrook, S.J., M.H. Carr, R.J. Schmitt and J.A. Coyer. 1990. The effect of giant kelp on local abundance of demersal fishes: the importance of ontogenetic resource requirements Bulletin of Marine Science 47:104-114.
117. Holbrook, S.J., M.J. Kingsford, R.J. Schmitt and J.S. Stephens Jr. 1994. Spatial and temporal patterns in assemblages of marine reef fish. *American Zool.* 34:463-475.
118. Holbrook, S.J., R.J. Schmitt and J.S. Stephens Jr. 1997. Changes in an assemblage of temperate reef fishes associated with a climate shift. Ecological Applications 7:1299-1310.
119. Holbrook, S.J., S.L. Swarbrick, R.J. Schmitt and R.F. Ambrose. 1993. Reef architecture and reef fish: correlations of population densities with attributes of subtidal rocky environments. Pp. 99-106 in: C.N. Battershill., D.R. Schiel, G.P. Jones, R.G. Creese, and A.B. MacDiamid (eds.), Proceedings of the Second International Temperate Reef Symposium, National Institute of Water and Atmospheric Research, New Zealand Oceanographic Institute.
120. Howarth, R.W. and others. 1997. Regional nitrogen budgets and riverine N and P fluxes for the drainages to the North Atlantic Ocean: Natural and human influences. Biogeochemistry 35: 75-139.
121. Incze, L. S., L. M. Mayer, E. Sherr, & S. Macko. 1982. Carbon inputs to bivalve mollusks: a comparison of two estuaries. Canadian Journal of Fisheries and Aquatic Science 39: 1348-1352.
122. Irvine, K N and G W. Pettibone. 1996. Planning level evaluation of densities and sources of indicator bacteria in mixed land use watershed.
123. Jackson, G. A. 1977. Nutrients and the production of giant kelp *Macrocystis pyrifera* off souther California. Limnology and Oceanography 22:979-995.
124. Jannasch, H.W., C.M. Sakamoto and T. Dickey 1996, High resolution nutrient variability in the Sargasso Sea. Presented at the 1996 AGU Ocean Sciences Meeting, San Diego CA.
125. Jannasch, H.W., K.S. Johnson and C.M. Sakamoto, 1994, Submersible, osmotically pumped analyzers for continuous determination of nitrate *in situ*. Analytical Chemistry, 66, 3352-3361.
126. Jellison, R., R.F. Anderson, J.M. Melack and D. Heil. 1996. Organic matter accumulation in sediments of hypersaline Mono Lake during a period of changing salinity. Limnol. Oceanogr. 41: 1539-1544.
127. Jellison, R., S. MacIntyre and F. Millero. 1999. The density characteristics of Mono Lake brine. Int. J. Salt Lake Res. In press.
128. Jellison, R.S., J. Romero and J.M. Melack. 1998. The onset of meromixis during restoration of Mono Lake, California: unintended consequences of reducing water diversions. Limnol. Oceanogr. 43:706-711.
129. Jenkins, T. M. Jr., S. Diehl, K. W. Kratz, and S. D. Cooper. 1999. Effects of population density on individual growth of brown trout in streams. Ecology 80: 941-956.
130. Johanson, R.C., J.C. Imhoff and H.H. Davis. 1980. User's manual for hydrologic simulation program: Fortran (HSPF) USEPA
131. Johnes, P.J. 1996. Evaluation and management of the impact of land use change on the nitrogen and phosphorus load delivered to surface waters: the export coefficient modeling approach. J. Hydrology 183: 33-349.

132. Johnson, D. L. 1980. Episodic vegetation stripping, soil erosion and landscape modification in prehistoric and recent historical time, San Miguel Island, California. pages 103-121, *In*: D. M. Power (editor), *The California Islands: Proceedings of a Multidisciplinary Symposium*. Santa Barbara Museum of Natural History, Santa Barbara, CA
133. Johnson, K.S. F. P. Chavez and G.E. Friederich. 1999. Continental –shelf sediment as a source of iron for coastal phytoplankton. *Nature* 398:697-700.
134. Jordan, T. E., D. L. Correll, J. Miklas, and D. E. Weller. 1991. Nutrients and chlorophyll at the interface of a watershed and an estuary. *Limnol. Oceanogr* 36: 251-267
135. Junak, S., T. Ayers, R. Scott, D. Wilken, & D. Young. 1995. A flora of Santa Cruz Island. Santa Barbara Botanic Garden, 397 pp. Kandt, D. J., D. D. Endicott and R. G. Kreis, Jr. 1993. Incorporating zebra mussels into food chain bioaccumulation models for the Great Lakes. 36<sup>th</sup> Conference Of The International Association For Great Lakes Research, June 4-10. p. 96
136. Keeley, J.E., C.J. Fotheringham, M. Morais. 1999. Reexamining fire suppression impacts on brushland fire regimes. *Science* 284: 1829-1832.
137. Keller, E.A., and Capelli, M.H., Ventura River flood of February 1992: A lesson ignored?: *Water Resources Bulletin*, v. 28, p. 813-832.
138. Kendall, B. E., C. J. Briggs, W. W. Murdoch, P. Turchin, S. P. Ellner, E. McCauley, R. M. Nisbet, and S. N. Wood. 1999. Why do populations cycle? A synthesis of statistical and mechanistic modeling approaches. *Ecology*, in press.
139. Kendall, C. 1998. Tracing nitrogen sources and cycling in catchments. Pages 519 to 576. In C. Kendall and J.J. McDonnell (eds.) *Isotope Tracers in Catchment Hydrology*. Elsevier Science
140. Kendall, C. and others. 1995. Tracing sources of nitrate in snowmelt runoff using oxygen and nitrogen isotopic compositions of nitrate. *IAHS Publ. no. 228*: 339-347
141. Kennedy, J.A., and Brassell, S.C., 1992, Molecular stratigraphy of the Santa-Barbara Basin - Comparison with historical records of annual climate change: *Organic Geochemistry*, v. 19, p. 235-244.
142. Kenyon, K. W. 1969. The sea otter in the eastern Pacific Ocean. *North American Fauna* 68:1-352.
143. Kratz, K. 1997. Predator-prey interactions in the benthos of high altitude streams. Dissertation, University of California, Santa Barbara.
144. Kratz, K. 1996. Effects of stoneflies on local prey populations: mechanisms of impact across prey density. *Ecology* 75: 1573-1585.
145. Leet, W. S., C. M. Dewees, C. W. Haugen, 1992. California's living marine resources and their utilization. California Sea Grant. Sea Grant Extension Publication UCSGEO-92-12.
146. Leonard, GH. 1999 Positive and negative effects of intertidal algal canopies on recruitment and survival of barnacles *Marine Ecology Progress Series* 178:241-249
147. Leonard, GH; Ewanchuk, PJ; Bertness, MD. 1999. How recruitment, intraspecific interactions, and predation control species borders in a tidal estuary *Oecologia* 118:492-502.
148. Leonard, GH; Levine, JM; Schmidt, PR; Bertness, MD. 1998 Flow-driven variation in intertidal community structure in a Maine estuary *Ecology*, 79:1395-1411.
149. Lika, K., Nisbet, R. M. A dynamic energy budget model based on partitioning of net production. *Journal of Mathematical Biology*, submitted.
150. Linden, O. 1976. Effects of oil on the reproduction of the amphipod Gammarus oceanicus. *Ambio* 5: 36-37.
151. MacIntyre, S., and J.R. Romero. 1999. Predicting upwelling, boundary mixing, and nutrient fluxes in lakes. *Verh. Internat. Verein. Limnol.* In press
152. MacIntyre, S., K. Flynn, J.S. Jellison and J. Romero. 1999. Boundary mixing and nutrient fluxes in Mono Lake, California. *Limnol. Oceanogr.* 44: 512-529.
153. Maidment, D.R., 1995, *GIS & Hydrology: User Notes for 15th Annual ESRI User Conference*, May 21, Palm Springs.
154. Mann K. H. 1973. Seaweeds: their productivity and strategy for growth. *Science* 182:975-981.

155. McCarthy, J. F. and L. R. Shugart. 1990. Biomarkers of Environmental Contamination. Lewis Publishers, Boca Raton, FL.
156. McCauley, E. Nisbet, R.M., DeRoos, A.M., Murdoch, W.W. and Gurney, W.S.C. 1996. Structured population models of herbivorous zooplankton. *Ecological Monographs* 66: 479-501.
157. McClelland, J.W., I. Valiela and R.H. Michener. 1997. Nitrogen stable isotope signatures in estuarine food webs: record of increasing urbanization in coastal watersheds. *Limnol.Oceanogr.*
158. McGowan JA; Cayan, DR; Dorman, LM. 1998. Climate-ocean variability and ecosystem response in the Northeast Pacific. *Science* 281:210-217
159. Melack, J.M. 1995. Transport and transformations of phosphorus in fluvial and lacustrine ecosystems. Pages 245-254 In H. Tiessen (ed.) Phosphorus cycling in terrestrial and freshwater ecosystems. SCOPE, John Wiley & Sons, New York
160. Melack, J.M. and J.O. Sickman. 1986. Major solute chemistry of stream water and rain in a southern California chaparral watershed. Proc. Chaparral Conference, California Water Resources Center Report 62:81-87.
161. Melack, J.M. and R. Jellison. 1998. Limnological conditions in Mono Lake: Contrasting monomixis and meromixis in the 1990s. *Hydrobiologia* 384:21-39.
162. Menge, B., A. Bryon, A. Daley, P. A. Wheeler P. T. Strun. 1997. Rocky intertidal oceanography: an association between community structure and phytoplankton concentrations *Limnology and Oceanography* 42: 57-66.
163. Menge, B.A. and J.S. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition and temporal heterogeneity. *American Naturalist* 110:351-369.
164. Menge, B.A. and J.S. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Naturalist* 130:730-757.
165. Mertes, L.A.K., in press, Documentation and significance of the perirheic zone on inundated floodplains: Water Resources Research.
166. Mertes, L.A.K., M.O. Smith and J.B. Adams, 1993, Estimating suspended sediment concentrations in surface waters of the Amazon River from Landsat images. *Int J. Rem. Sens.*, 43, 281-301.
167. Mertes, LAK; Hickman, M; Waltenberger, B; Bortman, AL; and others. 1988. Synoptic views of sediment plumes and coastal geography of the Santa Barbara Channel, California. *Hydrological Processes*, 12:967-979.
168. Meyer, J.L., W.H. McDowell, T.L. Bott, J.W. Elwood, C. Ishizaki, J.M. Melack, B. Peckarsky, B. Peterson and P. Rublee. 1988. Elemental dynamics in streams. *J.N. Am. Benthol. Soc.* 7:410-432.
169. Miller, P. A., K. R. Munkittrick and D. G. Dixon. 1992. Relationship between concentrations of copper and zinc in water, sediment, benthic invertebrates, and tissues of white sucker (*Catostomus commersoni*) at metal-contaminated sites. *Can. J. Fish. Aquat. Sci.*, 49: 978-984.
170. Miller, W. R. and J. I. Drever. 1977. Chemical weathering and related controls on surface water chemistry. *Geochimica et Cosmochimica Acta*, 41:1693-1702.
171. Milliman, J.D., and Syvitski, J.P.M., 1992, Geomorphic/Tectonic control of sediment discharge to the ocean: the importance of small mountainous rivers: *Journal of Geology*, v. 100, p. 525-544.
172. Morel, F. M. M., R. J. M. Hudson and N. M. Price. 1991. Limitation of productivity by trace metals in the sea. *Limnol. Oceanogr.*, 36: 1742-1755.
173. Murdoch, W.W. and Nisbet, R.M. 1996. Frontiers of population ecology. *In* Frontiers of Population Ecology (Eds. R.B. Floyd and A.W. Sheppard), pp. 31-43. CSIRO Press, Melbourne, Australia.
174. Murdoch, W.W., Nisbet, R.M., McCauley, E. De Roos, A.M., and Gurney, W.S.C. 1998. Plankton abundance across nutrient levels: tests of hypotheses. *Ecology*, 79: 1339-1356..

175. Neushul, M., W. D. Clarke, and D. W. Brown. 1967. Subtidal plant and animal communities of the southern California Islands. Pages 37-55 *In* R. Philbrick (editor) Proceedings of the symposium on the biology of the California Islands. Santa Barbara Botanic Garden, Santa Barbara, California.
176. Nisbet, R.M. 1997. Delay differential equations for structured populations *In* Structured Population Models (Eds. S. Tuljapurkar and H. Caswell ), pp. 89-118. Chapman and Hall
177. Nisbet, R.M. and Bence, J.R. 1989. Alternative dynamic regimes in canopy forming kelp: a variant on density-vague population regulation, *Am. Nat.* 134: 377-408.
178. Nisbet, R.M. and Wood, S.N. 1996. Estimation of copepod mortality rates. *Ophelia*, 44: 157-169.
179. Nisbet, R.M., de Roos, A.M., Wilson, W.G. and Snyder, R. 1998. Discrete consumers, small scale resource heterogeneity and population stability. *Ecology Letters* 1:34-37
180. Nisbet, R.M., Diehl, S., Wilson, W.G., Cooper, S.D., Donalson, D.D., and Kratz, K.. 1997 Primary productivity gradients and short-term population dynamics in open systems. *Ecological Monographs* 67: 535-553.
181. Nisbet, R.M., McCauley, E., Gurney, W.S.C., Murdoch, W.W., de Roos, A.M. 1997. Simple representations of biomass dynamics in structured populations *In* Case Studies in Mathematical Modeling: Ecology, Physiology, and cell Biology (Eds. H. G. Othmer, F. R. Adler, M.A. Lewis, and J.C. Dillon), pp. 61-79. Prentice Hall.
182. Nisbet, R.M., Ross, A.H. and Brooks, A.J. 1996. Empirically-based dynamic energy budget models: theory and an application to ecotoxicology. *Nonlinear World*, 3: 85-106.
183. Nisbet, R.M., S. Diehl, W.G. Wilson, S.D. Cooper, D.D. Donalson, and K. Kratz. 1997. Primary productivity gradients and short-term population dynamics in open systems. *Ecological Monographs* 67: 555-553.
184. Nixon, S. W. 1980. Between coastal marshes and coastal waters-a review of twenty years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry., p. 438-525. *In* P. Hamilton and K. MacDonald (eds) Estuarine and wetlands processes. Plenum.
185. Noonburg, E.G., Nisbet, R.M., McCauley, E., Gurney, W.S.C., Murdoch, W.W., de Roos, A.M. 1998. Experimental testing of dynamic energy budget models. *Functional Ecology*, 12: 211-212.
186. O'Brien, M. C. and P. A. Wheeler 1987. Short-term uptake of nutrients by *Enteromorpha prolifera* (Chlorophyceae). *J. Phycology* 23:547-556.
187. Oey, L-Y. 1996. Flow around a coastal bend: A model of the Santa Barbara Channel eddy. *J. Geophys. Res.* 101: 16,667-16,682.
188. Ohlmann, J.C., and D.A. Siegel, 1999: Ocean radiant heating: II., Parameterization and influence on sea surface temperature prediction. *J. of Physical Oceanography* (In press).
189. Ohlmann, J.C., D. A. Siegel, and C. Gautier, 1996: Ocean mixed layer radiant heating and solar penetration: A global analysis. *Journal of Climate*, 9, 2265-2280.
190. Ohlmann, J.C., D.A. Siegel, and C. Mobley, 1999: Ocean radiant heating: I., Optical influences. *In press Journal of Physical Oceanography*.
191. Ohlmann, J.C., D.A. Siegel, and L. Washburn, 1998, Radiant heating of the western equatorial Pacific during TOGA-COARE. *Journal of Geophysical Research*, 103, 5379-5395.
192. Oksanen, L. 1988. Ecosystem organization: mutualism and cybernetics or plain Darwinian struggle for existence? *American Naturalist* 131: 424-444.
193. Osenberg, C. W., R. J. Schmitt, S. J. Holbrook, and D. Canestro. 1992. Spatial scale of ecological effects associated with an open coast discharge of produced water. *in* "Produced Water" J. P. Ray and F. R. Engelhardt, editors, Plenum Press, New York. pp.387-402.
194. Osenberg, C.W., O. Sarnelle, S.D. Cooper, and R. D. Holt. 1999. Resolving ecological questions through meta-analysis: goals, metrics, and models. *Ecology* 80: 1105-1117.
195. Osenberg, C.W., O. Sarnelle, and S.D. Cooper. 1997. Effect size in ecological experiments: the application of biological models in meta-analysis. *American Naturalist* 150: 798-812.

196. Page, H. M. 1995. Variation in the natural abundance of  $^{15}\text{N}$  in the halophyte, *Salicornia virginica*, associated with groundwater subsidies of nitrogen in a southern California salt-marsh. *Oecologia* 104: 181-188.
197. Page, H. M. and D. M. Hubbard. 1987. Temporal and spatial patterns of growth in mussels *Mytilus edulis* on an offshore platform: relationships to water temperature and food availability. *Journal of Experimental Marine Biology and Ecology* 111: 159-179.
198. Page, H. M. in press. Importance of vascular plant and algal production to macroinvertebrate consumers in a southern California salt marsh. *Estuarine, Coastal and Shelf Science*.
199. Page, H. M., R. L. Petty, & D. E. Meade. 1995. Influence of watershed runoff on nutrient dynamics in a southern California salt marsh. *Estuarine, Coastal and Shelf Science* 41: 163-180.
200. Parmesan, C. 1996. Climate and species' range. *Nature* 382: 765-
201. Patterson, R.H., 1979, Tectonic geomorphology and neotectonics of the Santa Cruz Island Fault, Santa Barbara County, California. Dissertation, University of California, 141 p.
202. Pearse, J. S. and A. H. Hines. 1979. Expansion of a central California kelp forest following the mass mortality of sea urchins. *Marine Biology* 51:83-91.
203. Peckarsky, B.L., S.D. Cooper, and A.R. McIntosh. 1997. Extrapolating from individual behavior to populations and communities in streams. *Journal of the North American Benthological Society* 16: 375 - 390.
204. Pennings, S.C. 1993. Temporal and spatial variation in the recruitment of the sea hare, *Aplysia californica*, at Santa Catalina Island, California. Pp. 249-255 in: F.G. Hochberg (ed.), *Third California Islands Symposium. Recent Advances in Research on the California Islands*. Santa Barbara Museum of Natural History, Santa Barbara, CA.
205. Peterson, B. J. & B. Fry. 1987. Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics* 18: 293-320.
206. Peterson, B. J., R. W. Howarth, & R. H. Garritt. 1985. Multiple stable isotopes to trace the flow of organic matter in estuarine food webs. *Science* 227: 1361-1363.
207. Pinkel, R., M. Merrifield, M. McPhaden, J. Picaut, S. Rutledge, D. Siegel and L. Washburn, 1997: Solitary waves in the western Equatorial Pacific Ocean. *Geophysical Research Letters*, 24, 1603-1606.
208. Pitt, R. E. 1995. Effects of urban runoff on aquatic biota, in *Handbook of Ecotoxicology*, Hoffman, D. J., B. A. Rattner, G. Allen Burton, Jr. and J. Cairns, Jr. (eds.). Lewis Publishers, Boca Raton, FL
209. Platt, T. 1971. The annual production by phytoplankton in St. Margaret's Bay, Nova Scotia. *J. Cons. Cons. Int. Explor. Mer.* 33:324-333.
210. Power, M.E. 1990. Effects of fish in river food webs. *Science* 250:181-184.
211. Putnam, W.C., 1942, *Geomorphology of the Ventura Region, California*: Geological Society of America Bulletin, v. 53, p. 691-754.
212. Raimondi, P. T. and D. C. Reed. 1996. Determining the spatial extent of ecological impacts caused by local anthropogenic disturbances in coastal marine habitats, in R. J. Schmitt and C. W. Osenberg (eds.), *Detecting Ecological Impacts: Concepts and Applications in Coastal Habitats*. Academic Press.
213. Rainbow, P. S. 1995. Physiology, physicochemistry and metal uptake -- a crustacean perspective; in *Trace Metals in the Aquatic Environment, Proceedings Of The Third International Conference*. *Mar. Pollut. Bull.*, vol. 31: 55-59
214. Reed, D. C, D. R. Laur and A. W. Ebeling. 1988.. Variation in algal dispersal and recruitment: the importance of episodic events. *Ecological Monographs* 58:321-335.
215. Reed, D.C. 1990a. The effects of variable settlement and early competition on patterns of kelp recruitment. *Ecology* 71:776-787.
216. Reed, D.C. 1990b. An experimental evaluation of density dependence in a subtidal algal population. *Ecology*. 71:2286-2296.
217. Reed, D.C. and M. S. Foster. 1984. The effects of canopy shading on algal recruitment and growth in a giant kelp forest. *Ecology* 65:937-948.

218. Reed, D.C. and R.J. Lewis. 1994. Effects of an oil and gas production effluent on the colonization potential of giant kelp (*Macrocystis pyrifera*) zoospores. *Mar. Biol.* 119:277-83.
219. Reed, D.C., A.W. Ebeling, T.W. Anderson, and M. Anghera. 1996. Differential reproductive responses to fluctuating resources in two seaweeds with different reproductive strategies. *Ecology*. 77:300-316.
220. Reed, D.C., T.W. Anderson, A.W. Ebeling, and M. Anghera. 1997. The role of reproductive synchrony in the colonization potential of kelp. *Ecology* 78:2443-2457.
221. Reed, D.C., M.A. Brzezinski, D.A. Coury, W.M. Graham, and R.L. Petty. 1999. Neutral lipids in macroalgal spores and their role in swimming. *Marine Biology* 133:737-744 .
222. Reed, D.C., P.T. Raimondi, M.H. Carr and L. Goldwasser. The role of dispersal and disturbance in determining spatial heterogeneity in sedentary kelp-forest organisms. *Ecology in press*
223. Reed, D.C., R. J. Lewis, and M. Anghera. 1994. Effects of an open coast oil production outfall on patterns of giant kelp (*Macrocystis pyrifera*) recruitment. *Mar. Biol.* 120:26-31.
224. Richards, D. V., D. Gramlich, G.E. Davis, and M. McNulty. 1997. Kelp forest ecological monitoring, Channel Islands National Park 1982-1989. Technical Report CHIS-97-05. Channel Islands National Park, Ventura.
225. Riera, P. and P. Richard. 1996. Isotopic determination of food sources of *Crassostrea gigas* along a trophic gradient in the estuarine Bay of Marennes-Oleron. *Estuarine, Coastal and Shelf Science* 42: 347-360.
226. Rockwell, T.K., Keller, E.A., Clark, M.N., and Johnson, D.L., 1984, Chronology and rates of faulting of Ventura River terraces, California: *Geological Society of America Bulletin*, v. 95, p. 1466-1474.
227. Roll, S. K. 1998. The effects of a gradient of nutrient additions on levels of primary producers and consumers in Convict Creek, California. M.A. Thesis, University of California, Santa Barbara.
228. Romero, J., R. Jellison and J.M. Melack. 1998. Stratification, vertical mixing and upward ammonium flux in hypersaline Mono Lake, California. *Arch. Hydrobiol.* 142:283-315.
229. Romero, J.R. and J.M. Melack. 1996. Sensitivity of vertical mixing in a large saline lake to variations in runoff. *Limnol. Oceanogr.* 41: 955-965.
230. Roo, A.P.J., Hazelhoff, L., and Burrough, P.A., 1989, Soil erosion modelling using 'ANSWERS' and geographical information systems: *Earth Surface Processes and Landforms*, v. 14, p. 517-532.
231. Safran, E.B. and T. Dunne, Distribution and evolution of geomorphic process zones in the Eastern Cordillera of Bolivia, Third Internat. Symp. on Andean Geodynamics, St Malo (France), 741-744, 1996.
232. Safran, E.B., Channel network incision and patterns of mountain geomorphology. Dissertation, University of California Santa Barbara, 1998.
233. Sarnelle, O., K.W. Kratz and S.D. Cooper. 1993. Effects of an invertebrate grazer on the spatial arrangement of a benthic microhabitat. *Oecologia* 96: 208-218.
234. Schimel, J. 1995. Ecosystem consequences of microbial diversity and community structure. *In: Arctic and Alpine Biodiversity: patterns, causes, and ecosystem consequences*. F.S. Chapin and C. Korner (Eds.). Springer-Verlag, Berlin. pp. 239-254.
235. Schimel, J.P. 1996. Assumptions and errors in the  $^{15}\text{NH}_4^+$  pool dilution technique for measuring mineralization and immobilization. *Soil Biol. Biochem.* 28: 827-828.
236. Schimel, J.P. and J. Gulledege. 1998. Microbial Community Structure and Global Trace Gases. *Global Change Biology*. 4: 745-758.
237. Schimel, J.P. and J.S. Clein. 1996. Microbial response to freeze-thaw cycles in tundra and taiga soils. *Soil Biology and Biochemistry*. 28: 1061-1066.
238. Schimel, J.P. K. Van Cleve, R. Cates, T. Clausen, and P. Reichardt. 1996. Effects of balsam poplar (*Populus balsamifera*) tannins and low-molecular-weight phenolics on microbial activity in taiga floodplain soil: changes in N cycling during succession. *Can. J. Bot.* 74: 84-90.

239. Schimel, J.P., J.M. Gullledge, J.S. Clein-Curley, J.E. Lindstrom, and J.F. Braddock. 1999. Moisture effects on microbial activity and community structure in decomposing birch litter in the Alaskan taiga. *Soil Biology & Biochemistry*. 31: 831-838.
240. Schimel, J.P., R.G. Cates, and R. Ruess. 1998. The role of balsam poplar secondary chemicals in controlling soil nutrient dynamics through succession in the Alaskan taiga. *Biogeochemistry*. 42: 221-234.
241. Schimmelman, A., Lange, C.B., and Berger, W.H., 1990, Climatically-controlled marker layers in Santa-Barbara Basin sediments and fine-scale core-to-core correlation: *Limnology and Oceanography*, v. 35, p. 165-173.
242. Schlesinger, W.H. and J.M. Melack. 1981. Transport of organic carbon in the world's rivers. *Tellus* 33:172-187.
243. Schmitt, R.J. 1996. Exploitation competition in mobile grazers: trade-offs in use of a limited resource. *Ecology* 77: 407-425.
244. Schmitt, R.J. 1993. Geographic variation in population characteristics of an intertidal gastropod: Demographic differences or settlement history? Pp. 257-271 *in*: F.G. Hochberg (ed.), *Third California Islands Symposium. Recent Advances in Research on the California Islands*. Santa Barbara Museum of Natural History, Santa Barbara, CA.
245. Schmitt, R.J. and S.J. Holbrook. 1984a. Gape-limitation, foraging tactics and prey size selectivity of two microcarnivorous species of fish. *Oecologia* 63: 6-12.
246. Schmitt, R.J. and S.J. Holbrook. 1984b. Ontogeny of prey selection by black surfperch, *Embiotoca jacksoni* (Pisces: Embiotocidae): the roles of fish morphology, foraging behavior, and patch selection. *Marine Ecology, Progress Series* 18: 225-239.
247. Schmitt, R.J. and S.J. Holbrook. 1985. Patch selection by juvenile black surfperch (Embiotocidae) under variable risk: interactive influence of food quality and structural complexity. *Journal of Experimental Marine Biology and Ecology* 85: 269-285.
248. Schmitt, R.J. and S.J. Holbrook. 1986. Seasonally fluctuating resources and temporal variability of interspecific competition. *Oecologia* 69:1-11.
249. Schmitt, R.J. and S.J. Holbrook. 1990a. Density compensation by surfperch released from competition. *Ecology* 71: 1653-1665.
250. Schmitt, R.J. and S.J. Holbrook. 1990b. Contrasting effects of giant kelp on dynamics of surfperch populations. *Oecologia* 84:419-429.
251. Schmitt, R.J. and S.J. Holbrook. 1996. Local-scale patterns of larval settlement in a planktivorous damselfish - do they predict recruitment? *Journal of Marine and Freshwater Research* 47: 449-463.
252. Schmitt, R.J. and S.J. Holbrook. 1999. Settlement and recruitment of three damselfish species: larval delivery and competition for shelter space. *Oecologia* 118: 76-86.
253. Schmitt, R.J. and S.J. Holbrook. 1999. Mortality of Juvenile Damselfish: Implications for Assessing Processes that Determine Abundance. *Ecology* 80: 35-50.
254. Schmitt, R.J. and S.J. Holbrook. 1999. Temporal patterns of settlement of three species of damselfish of the genus *Dascyllus* (Pomacentridae) in the coral reefs of French Polynesia. *In*: Proc. 5th Indo-Pac. Fish Conf., Nouméa, 1997 (Séret B. & J.-Y. Sire, eds), pp. 537-551. Paris: Soc. Fr. Ichtyol.
255. Schmitt, R.J. and S.J. Holbrook. Habitat-limited Recruitment of Coral Reef Damselfish. *Ecology* (in review)
256. Scott, K.M., and Williams, R.P., 1978, Erosion and sediment yields in the Transverse Ranges, southern California, U.S.: USGS Professional Paper 1030, 37 p.
257. Seymour, R. J., M. J. Tegner, P. K. Dayton and P. E. Parnell. 1989. Storm wave induced mortality of giant kelp, *Macrocystis pyrifera*, in southern California. *Estuar. Coast. Shelf Sci.* 28:277-292.
258. Shipe, R.F., Brzezinski, M.A., Pilskaln, C., and Villareal, T.A. Species-specific phasing of silicon deposition in *Rhizosolenia* mats. *J. Phycol.* (in review).
259. Siegel, D.A., T. Westberry, and J.C. Ohlmann, 1999: On cloud color and ocean radiant heating. *Journal of Climate*, 12, 1101-1116.

260. Simenstad, C. A. & R. C. Wissmar. 1985.  $\delta^{13}\text{C}$  evidence of the origins and fates of organic carbon in estuarine and nearshore food webs. *Marine Ecology Progress Series* 22: 141-152.
261. Smith R C, J Marra, M J Perry, K S Baker, E Swift, E Buskey & D A Kiefer. 1989. Estimation of a photon budget for the upper ocean in the Sargasso Sea. *Limnol. Oceanogr.* 34: 1677-1697.
262. Soil Conservation Service. 1986. Urban hydrology for small catchments. USDA
263. Sousa, W. P. 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecological Monographs* 49:227-254.
264. Sousa, W. P. S. C. Schroeter, and S. D. Gaines. 1981. Latitudinal variation in intertidal algal community structure: the influence of grazing and vegetative propagation. *Oecologia* 48:297-307.
265. Stecher, H. A. III, D. E. Krantz, C. J. Lord III, G. W. Luther III and K. W. Bock. 1996. Profiles of strontium and barium in *Mercenaria mercenaria* and *Spisula solidissima* shells. *Geochimica et Cosmochimica Acta*, 60: 3445-3456.
266. Steele, M.A. 1995. The contributions of predation, competition, and recruitment to population regulation of two temperate reef fishes. PhD dissertation, U.C. Santa Barbara, Santa Barbara.
267. Steele, M.A. 1997. Population regulation by post-settlement mortality in two temperate reef fishes. *Oecologia* 112: 64-74.
268. Steele, M.A. 1998. The relative importance of predation and competition in two reef fishes. *Oecologia* 115: 222-232.
269. Stephenson, R. L. & G. L. Lyon. 1982. Carbon-13 in an estuarine bivalve: Detection of marine and terrestrial food sources. *Oecologia* 55: 110-113.
270. Strub, P.T., and C. James. 1995. The large-scale summer circulation of the California Current, *Geophys. Res. Lett.* 22, 3: 207-210.
271. Strub, P.T., P.M. Kosro, and A. Huyer. 1991. The nature of cool filaments in the California Current
272. Stumpf, R.P., and J.R. Pennock, 1989, Calibration of a general optical equation for remote sensing of suspended sediments in a moderately turbid estuary. *Journal of Geophysical Research*, 94, 14363-14371.
273. Sugai, S.F. and J.P. Schimel. 1993. Decomposition and biomass incorporation of  $^{14}\text{C}$ -labeled glucose and phenolics in taiga forest floor: effect of substrate quality, successional state, and season. *Soil Biol. Biochem.* 25: 1379-1389
274. T. Dunne, Critical data requirements for prediction of erosion and sedimentation in mountain drainage basins, *J. Amer. Water Works Association*, 34, 795-808, 1998.
275. Taylor, P. and S. D. Gaines. 1999. Can Rapoport's Rule be Rescued: Modeling possible causative mechanisms of the latitudinal gradient in species diversity. *Ecology*. In press.
276. Tegner, M. J., and P. K. Dayton. 1987. El Niño effects on southern California kelp forest communities. *Advances in Ecological Research*. 17:243-279.
277. Toole, D.A., and D.A. Siegel, 1999: Empirical and mechanistic approaches to understanding ocean color variability in the Santa Barbara Channel. To be submitted to *Journal of Geophysical Research*.
278. Torsvik, V., F.L. Daae, R-A. Sandaa, L. Ovreas. 1998. Novel techniques for analysing microbial diversity in natural and perturbed environments. *Journal of Biotechnology*. 64: 53-62.
279. Triska, F.J. and others. 1989. Retention and transport of nutrients in a third-order stream in northwestern California: hyporheic processes. *Ecology* 70: 1893-1905.
280. Valentine, J. W. 1966. Numerical analysis of marine molluscan ranges on the extratropical northeastern Pacific shelf. *Limnology and Oceanography* 11: 198-211.
281. VanBlaricom, G. R. and J. A. Estes. 1988. The community ecology of sea otters. Springer-Verlag, Berlin.
282. Villareal, T.A., Pilskaln, C., Brzezinski. M.A., Lipschultz, F. and Gardner G.B. (1999) Upward transport of oceanic nitrate by migrating diatom mats. *Nature* 397: 425-427.

283. von Westernhagen, H. R., V. Dethlefsen, W. Ernest, U. Harms, and P. D. Hansen. 1981. Bioaccumulating substances and the reproductive success in Baltic flounder Platichthys flesus. *Aquatic Toxicology* 1:85-99.
284. Wagener, S.M. and J.P. Schimel. 1998. Stratification of soil ecological processes: a study of the birch forest floor in the Alaskan taiga. *Oikos*. 81: 63-74.
285. Wagener, S.M., M.W. Oswood, and J.P. Schimel. 1998. River and soil continua: Parallels in carbon and nutrient processing. *Bioscience*. 48: 104-108.
286. Weaver, R.W. and others (eds.). 1994. *Methods of Soil Analysis. Part 2: Microbiological and biochemical properties*. Soil Science Society of America. Madison.
287. Wheeler, P.A. and W. J. North. 1981. Nitrogen supply, tissue composition and frond growth rates for *Macrocystis pyrifera*. *Marine Biology* 64:59-69.
288. Wilson, W.G., Osenberg, C.W., Schmitt, R.J., and Nisbet, R.M. Complementary foraging behavior allows co-existence of two grazers. *Ecology*, (in press).
289. Wiseman, S.W., S.D. Cooper and T.L. Dudley. 1993. The effects of trout on epibenthic odonate naiads in stream pools. *Freshwater Biol.* 30: 133-145.
290. Wood, S.N. (1999). Partially specified population models: modeling, data fitting and inference with incomplete ecological information. Submitted to *Ecology*.
291. Woolhiser, D.A., R.E. Smith and D.C. Goodrich. 1990. KINEROS, Kinematic runoff and erosion model: Documentation and user manual. USDA-ARS
292. Worcester, S. and S. D. Gaines. 1997. Quantifying hermit crab recruitment rates and larval shell selection on wave swept shores. *Marine Ecology Progress Series*. 157:307-310.
293. Yankovich, T. L. and R. D. Evans. 1995. The relative importance of the dissolved and particulate phases in cadmium uptake by the freshwater bivalve, *Elliptio complanata*. *Proceedings Of The 38th Conference Of The International Association Of Great Lakes Research., International Association For Great Lakes Research, Ann Arbor, Mi*
294. Zimmerman, R. C. and J. N. Kremmer. 1984. Episodic nutrient supply to a kelp forest ecosystem in southern California. *J. Mar. Res.* 42:591:604.
295. Zimmerman, RC, Reguzzoni JL, Alberte RS. 1995. Eelgrass (*Zostera marina* L.) transplants in San Francisco Bay: role of light availability on metabolism, growth and survival. *Aquat. Bot.* 51:67-86.

## ***Section 4 -- Research Management Plan***

The research management plan for the Santa Barbara Land-Ocean LTER program encompasses several important focal areas, including internal project governance, project resource allocation and acquisition, day-to-day running of the project, site plan and preservation, agency relations (including NSF) and interactions with the LTER network of sites. The PI (Reed) and Co-PIs (Melack, Gaines, Holbrook and Cooper) and three associate investigators (Brzezinski, Reichman, and Schimel) and will form an executive council that will make most of the program's policy and resource decisions and will interact with the agency and the LTER network of sites. The eight member council will greatly streamline the decision making process as it will be difficult to get all 22 investigators together on regular intervals. The choice of eight members on the executive council will insure that there will be a representative for land, freshwater, reef, ocean, and data management issues as well as for ecosystems and physicochemical factors. The executive council will focus upon allocation of agency resources and staffing for the project, as well as the group's response to new research opportunities (such as a NSF instrumentation grant or a focus research opportunities). A program director will be designated as a single point of contact for agency, LTER network and university activities. Initially, this person will be Dr. Daniel Reed. Issues that are deemed to be critical, such as the designation of a new director or the addition or subtraction of associate investigators, will be decided by all the primary investigators (PI, co-PIs and associate investigators). The director and the executive council will be assisted by a full-time administrative assistant.

The day-to-day running of our Land-Ocean LTER will be done by several professional staff members. A staff research associate will act as coordinator for all field work activities (FWC) and a computer network technologist will work as the project's database manager (DBM). The FWC will work with the administrative assistant to coordinate all field work logistics and data entry, and will insure that finished data sets are passed on to the DBM. The DBM will work closely with Drs. James Frew (Bren School of Environmental Science and Management) and James Reichman (Director of the National center for Ecological Analysis and Synthesis (NCEAS)) who will oversee the design of the database and its management. Both the FWC and the DBM will report to the program director and will attend executive council meetings (if appropriate). The DBM will be the single point of contact for interactions with database managers at the other LTER sites.

We are presently planning to hold an all-day LTER retreat for all LTER participants each year to insure coordination across the LTER program and to enhance interdisciplinary discussions. All PIs, associate investigators, staff and students will attend this annual meeting. Agency, LTER and university representatives will be invited to this meeting. We will also hold quarterly meetings of all participants to insure that all relevant matters are brought forward. This will also enhance the cross-disciplinary development of ideas and approaches. This especially will be useful for the graduate students supported on this (or related) grant. The fact that initially all investigators are from UCSB will insure a good deal of interaction among participants.

We are very fortunate that our core sites have restricted public access. The University of California Natural Reserve System, Channels Islands National Park, Channels Islands National Marine Sanctuary, and Santa Barbara County are all active participants in the Santa Barbara Channel LTER. The restricted public access and on-going monitoring activities will insure that our sites remain accessible to us and relatively undisturbed by others throughout the duration of this program.

## ***Section 5 -- Information Management and Metadata Standards***

### **Data Sharing and Public Availability**

We believe that federally funded data are public property and should be available to all without restrictions. Our default policy will be to make field data available on the (World Wide) Web as soon as we verify its quality, certainly within 1 year of acquisition. Exceptions to the default availability policy may fall into three categories: proprietary third-party information, short-term “blackout” periods for student research, and experimental results. Proprietary information will be stored in the system only if its security can be reasonably guaranteed, and only if it is crucial to LTER research. “Blackout” periods will be allowed only while students complete their theses. In either case, the restricted information must still be internally accessible, under the same data quality and consistency constraints as unrestricted information. Finally, in the case of experiments, raw data will not be required not be placed on the web, but data from completed experiments will be made available. We may withhold LTER support from investigators that gratuitously withhold data.

All data will be given to a full-time database manager (DBM) who will perform quality assurance checks, and ensure that it meet proper format and meta-data standards before making it available over the web. This will insure the steady flow of data into our LTER database. Since our purpose is to support cutting-edge, interdisciplinary ecological research, it is in our best interests to enable all investigators to use our data to perform new and exciting science. Open access via the Web will make our data available for use by the widest range of our peers, insuring NSF the best return on its investment.

### **Information Management Strategy**

We will specify our information management (IM) system's capabilities in terms of generic interfaces *documentation*, *search*, and *retrieval*, which can be implemented by many underlying technologies (Web servers, SQL databases, etc.) These interfaces will be implemented by modular, cooperating components (function libraries, database schemata, CGI scripts, etc.), which will necessarily depend on specific underlying technologies, and will thus be designed to have as little impact on the rest of the system as possible. For example, a component that delivers GIS coverages as lists of vector endpoints should not affect how the rest of the system deals with GIS coverages.

Our heterogeneous data and analysis requirements, and the distributed resources already available to our researchers, argue against a single centralized system. The storage and processing requirements of our datasets vary by orders of magnitude; e.g., a single Landsat image is larger than all the species count data we could ever conceivably collect. Software packages may be tied to only a few hosts by licensing or other restrictions, and these hosts may in turn be remote from our online archives. Our IM needs will thus best be served by a distributed services infrastructure, which can knit these components together as effortlessly as possible.

### **Documentation Services**

We will support three basic documentation services: browsing of HTML text delivered by HTTP (Web) servers; Web-based thesauri to map between domain-specific terminology and our internal metadata standards; and a subscription service to alert researchers to changes in our collections and services. Since we assume all LTER researchers will have personal Web servers (i.e. their own “Web sites.”), the documentation services can be highly distributed.

### **Search Services**

Three basic search services will support locating specific data holdings within the Santa Barbara LTER site IM system: HTML forms-based queries against search engines and SQL databases; custom HTTP-based search interfaces; and Z39.50 searches using the

GEO attribute set. Forms-based queries should be adequate for simple searches of unstructured data, as well as for general queries such as “do you have any data for 1998?” Custom HTTP-based interfaces will be used internally to connect our search capabilities to specific tools. A Z39.50 server will respond to GEO attribute set queries (the standard for the U.S. National Spatial Data Infrastructure.) We will match services to specific client requirements, rather than invent entire new end-to-end solutions.

### **Retrieval Services**

We will support three basic retrieval services: “raw” data streams over FTP connections; MIME-typed data streams over HTTP connections; and processed data streams over HTTP connections, via methods encoded as URLs. Raw data will be delivered without any processing, in standard formats such as HDF, XML, and CSV. MIME-typed data will be delivered to specific client applications (e.g., shape files to a GIS.) Custom HTTP-based interfaces will be used to access server-side preprocessing such as subsetting (e.g. SQL SELECTs, array hyperslab extraction, etc.).

### **Metadata Standards**

Our primary metadata standards will be the Ecological Metadata Language (EML) and the Biological Data Profile of the FGDC Content Standard for Digital Geospatial Metadata. These standards are already used extensively at UCSB and NCEAS. To allow our metadata standards to evolve over time, we will ensure that: our internal standards are fully documented; our search and retrieval services support appropriate external standards; our documentation services include thesauri for the standard terminology we support; and all our services can migrate to new internal and external standards.

### **Conclusion**

The IM system we propose can be assembled today from off-the-shelf technologies. While the components are (deliberately) not “bleeding-edge”, their application, specifically in support of multiple, distributed search, retrieval, and documentation services, is novel, and will advance the state of the art in LTER data management.

UCSB is ideally suited to undertake the IM system for this LTER project. The campus hosts several pertinent centers and projects as well as participating in UC-wide informatics efforts. The IM system will be coordinated by Dr. James Frew (Donald Bren School of Environmental Science and Management) and Dr. James Reichman (Director of NCEAS.) Dr. Frew has extensive experience with environmental information management, particularly relating to storage and retrieval of spatially referenced data. Scientists visiting NCEAS use existing information to address important ecological questions. NCEAS has developed several tools and methods for heterogeneous data and thus has experience with how investigators assimilate and employ this information. The combination of technical skills and experience with a wide range of data make this an effective team to coordinate the information management for this project.

## FACILITIES, EQUIPMENT & OTHER RESOURCES

---

**FACILITIES:** Identify the facilities to be used at each performance site listed and, as appropriate, indicate their capacities, pertinent capabilities, relative proximity, and extent of availability to the project. Use "Other" to describe the facilities at any other performance sites listed and at sites for field studies. USE additional pages if necessary.

### **Laboratory:**

The principal investigators have laboratory space in the Department of Ecology, Evolution and Marine Biology (DEEMB), Department of Geography, the Donald Bren School of Environmental Science and Management, and the Marine Science Institute at UCSB that is sufficient for the project's needs. We will also have access to common laboratory space in DEEMB's marine biotechnology building, including environmentally controlled temperature rooms that are supplied with three different temperatures of running seawater. The Marine Science Institute's Analytical Laboratory is a professionally managed shared-use instrumentation and chemical analysis facility that is well equipped to perform all of the chemical analyses anticipated for this project. Major capabilities of the Lab include elemental analysis of inorganic and organic substances, stable isotope ratio determination of biological materials, and automated determination of nutrients in natural waters.

**Clinical:** not required for this project

**Animal:** not required for this project

### **Computer:**

Each of the investigators in this project maintain computing capabilities commensurate with their specific research activities. Dr. Frew, who will collaborate on the informatics portion of this project, will have access to more than 60 UNIX workstations connected to a common high-speed switched Ethernet at the UCSB Institute for Computational Earth System Science (ICESS). Total disk storage has recently been expanded to nearly 2 Terabytes and a full complement of database, computational, image processing, statistical and scientific visualization software are available for use. ICESS also operates a TeraScan satellite receiving and analysis station which will be used by Dr. Siegle to acquire AVHRR sea surface temperature and SeaWiFS ocean color imagery. Data management for the project will have the advantage of utilizing the computing capabilities of NCEAS under the direction of Dr. Reichman. The Center maintains a heterogeneous, networked computing environment available to resident and visiting scientists and to this LTER project. The internal backbone consists of 10 and 100 Mbps switched ethernet. Internet connectivity is achieved via a dedicated T1 connection to the UCSB campus. NCEAS' technical staff are participating in campus planning for the CalRen-II network, which will bring OC-3 (155 Mbps) and eventually OC-12 (622 Mbps) connectivity to UCSB as part of the NSF-sponsored vBNS. NCEAS maintains two high-end database and analytical servers: a Silicon Graphics Origin 2000, with four R10K CPU's, and 1.5 GB of RAM; and an SGI Power Challenge L, with four R10K CPU's, and 1.5 GB of RAM. Storage includes over 45 GB online disk storage and a 75 GB robotic DLT tape backup system. All servers are archived nightly, and are on uninterruptible power supplies. High-end PCs, Macintoshes, and UNIX workstations are available to resident and visiting researchers. Planned upgrades with direct relevance to supporting an informatics venture include addition of a large, high-availability storage system, RAM upgrades for the servers, and an automated high-volume, high-speed tape backup system. NCEAS supports a number of scalable software packages, including SAS, MATLAB, Splus, CPLEX, ArcInfo and ArcView, and parallelizable compilers for

Fortran 90, Fortran 77, C++, and C. Oracle, running on our SGI Power Challenge, is our primary database server.

**Office:**

All principal investigators, associate investigators, have adequate office space to meet their needs and those of the post docs and graduate students associated with this project. All offices are equipped with phone and internet services.

**Other:**

Special facilities are not required at our field sites, which are all located close to campus.

---

**MAJOR EQUIPMENT:** List the most important items available for this project and, as appropriate identifying the location and pertinent capabilities of each.

Most chemical analyses will be done using instrumentation in MSI's Analytical Laboratory. Major equipment in this lab include: two atomic absorption spectrophotometers (AAS) with auto samplers, one instrument equipped for flame atomization, and the other a dedicated furnace system with Zeeman background correction; a microprocessor-controlled gas chromatograph (GC) with various detectors, including flame ionization and photo-ionization; two automated organic elemental analyzers for CHN analyses, an isotope ratio mass spectrometer interfaced with a CHN sample introduction system, and an automated 5-channel wet-chemical analyzer (FIA) for nutrients. The laboratories of several investigators are equipped with additional instrumentation that will be used to do the proposed work including: a liquid scintillation counter for analysis of samples from measurements of primary production using  $^{14}\text{C}$  (Brzezinski), a gas chromatograph/mass spectrophotometer for analyzing organics (Holden), a Lachat Autoanalyzer, C/N analyzer, gas chromatograph, and an infrared gas analyzer to be used in nutrient analyses and soil chemistry (Schimel). Oceanographic instrumentation available to this project include: a CTD, four acoustic Doppler current profilers and one acoustic Doppler velocitometer for measuring currents in the water column, five high-frequency radar units (Coastal Ocean Dynamics Applications Radars, CODAR) for measuring surface currents, and a minibat undulating towed fish for measuring physical and biological properties of the water column (Gaines, Warner, Washburn).

---

**OTHER RESOURCES:** Provide any information describing the other resources available for the project. Identify support services such as consultant, secretarial, machine shop, and electronics shop, and the extent to which they will be available for the project. Include an explanation of any consortium/contractual arrangements with other organizations.

UCSB has the facilities and trained technical staffs typical of large universities. Resources that will be of most value to this project include, machine, electronic, and carpentry shops for constructing apparatus for the laboratory and field, a large capacity seawater system, which is currently being upgraded for expanded use, a fleet of small vessels that are maintained by a certified boat mechanic, and a research diving program that includes ~ 60 scuba tanks, and a compressor and technician to fill them. Use of university equipment, and consultant and technician services are available to us, generally on a recharge basis.

---