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NSF 03-599 **01/13/04**

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TITLE OF PROPOSED PROJECT **LTER: Long-Term Dynamics of a Coral Reef Ecosystem**

REQUESTED AMOUNT	PROPOSED DURATION (1-60 MONTHS)	REQUESTED STARTING DATE	SHOW RELATED PRELIMINARY PROPOSAL NO. IF APPLICABLE
$ **4,860,209**	**72** months	**09/01/04**	

CHECK APPROPRIATE BOX(ES) IF THIS PROPOSAL INCLUDES ANY OF THE ITEMS LISTED BELOW

☐ BEGINNING INVESTIGATOR (GPG I.A)
☐ DISCLOSURE OF LOBBYING ACTIVITIES (GPG II.C)
☐ PROPRIETARY & PRIVILEGED INFORMATION (GPG I.B, II.C.1.d)
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☐ SMALL GRANT FOR EXPLOR. RESEARCH (SGER) (GPG II.D.1)
☒ VERTEBRATE ANIMALS (GPG II.D.5) IACUC App. Date **10/28/03**
☐ HUMAN SUBJECTS (GPG II.D.6)
Exemption Subsection ________ or IRB App. Date ________
☐ INTERNATIONAL COOPERATIVE ACTIVITIES: COUNTRY/COUNTRIES INVOLVED (GPG II.C.2.j)
☒ HIGH RESOLUTION GRAPHICS/OTHER GRAPHICS WHERE EXACT COLOR REPRESENTATION IS REQUIRED FOR PROPER INTERPRETATION (GPG I.E.1)

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Intellectual Merit. This proposal is to establish a Long-Term Ecological Research (LTER) site focused on dynamics of coral reef ecosystems, at the island of Moorea, French Polynesia, location of the University of California's Gump Research Station. Coral reefs are of great ecological importance, having the highest species diversity of any marine habitat and ranking near the top of all ecosystems with respect to annual total gross productivity. The communities are supported structurally by reef-building corals and trophically by efficient recycling. Unlike highly productive terrestrial ecosystems, the key biotic interaction underlying reef systems is the mutualistic relationship between hermatypic corals and photosynthetic zooxanthellae. Hermatypic corals are both functional autotrophs and heterotrophs and derive carbon from multiple sources. In addition to biotic interactions, numerous other biological processes are influenced by a variety of abiotic events that can operate at spatial scales ranging from millimeters to hundreds of kilometers, and which can vary on short to long time scales. Coral reef ecosystems can be affected by perturbations ranging from short and relatively localized disturbances, where return to the original state is possible, to more chronic, widespread influence of shifts in climate over decades that may fundamentally alter the ecosystem. The latter perturbation is predicted to cause sweeping change in coral reef ecosystems in the coming decades. While there are coral reef monitoring programs, descriptive ecology alone cannot elucidate the mechanistic basis of change in these systems.

Because of the complexity of coral reef ecosystems, there is an incomplete understanding of the processes that collectively determine their structure, function and dynamics. The proposed LTER will estimate long-term trends and address key gaps in understanding through long-term observations and experiments supplemented by shorter-term process studies. The goals are to better understand key processes that (i) modulate ecosystem function, (ii) shape community structure and diversity, and (iii) determine abundance and dynamics of constituent populations. Such mechanistic understanding will allow more accurate predictions of how coral reef ecosystems will respond to qualitatively different types of environmental change. Coordinated interdisciplinary research by the team of 20 investigators will address issues central to the LTER program. The themes that will form the core research thrusts of the proposed LTER include: (1) the biological bases for variation in ecological performance of hermatypic corals (the foundational group); (2) population dynamics of key groups; (3) food web and nutrient dynamics; and (4) the maintenance and functional consequences of diversity. Two additional research components cut across these themes and will help to integrate and generalize the research endeavors of the thematic areas. These are: (a) an explicit focus on physical – biological coupling (including but not limited to abiotic forcing) over multiple scales; and (b) hydrodynamic, food-web and ecosystem modeling to obtain greater insight and predictive power, and to further guide empirical efforts. Major issues within each thematic area will be addressed through focused, process-oriented studies and by long-term monitoring of key abiotic conditions and important ecosystem processes, community attributes, and demographic processes for representative functional groups of organisms.

Broader Impacts. Both the scientific community and the public have tremendous interest in and concern about conservation of coral reef ecosystems. The proposed project will greatly increase understanding of these systems, and as such, will inform government officials, resource managers and others charged with conservation and management of coral reefs. LTER cross-site comparisons that reveal generality across different ecosystems will lead to more effective management of natural resources in general. Scientific findings and technical information from the project will be broadly disseminated through a website, scientific publications and presentations, and in the media. Outreach activities will be extensive, and will involve K-12 programs in Southern California as well as community and school outreach in French Polynesia and an internship program for Tahitian university students (coordinated by the Atitia Center). Undergraduate and graduate students from underrepresented groups (particularly Hispanic, Native American and Pacific Island) will be involved in an education and research training program, linking California State University Northridge (a minority institution) and University of California Santa Barbara, that will provide training in research, team research experiences, and development of skills needed to carry out interdisciplinary, collaborative research. The project also will engage in post-doctoral training, and will build international linkages between US scientists and those in South Pacific island nations.

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INTRODUCTION

A central goal of the Long-Term Ecological Research program is to advance understanding of ecological phenomena within and among ecosystems that occur over long periods of time and ranges of spatial scales. Core research issues addressed at LTER sites include (i) dynamics and control of primary production, (ii) population dynamics of representative groups, (iii) pattern and control of organic recycling, (iv) pattern of inorganic input and nutrient dynamics, and (v) patterns and consequences of disturbances that arise from or induce long-term trends. Cross-site comparisons are facilitated through initiatives on such themes as the consequences of biodiversity losses, ecosystem effects of climate change, and landscape-level changes arising from long-term environmental change.

Here we propose a coral reef ecosystem LTER site at Moorea, French Polynesia ('Tahiti'), where the University of California operates a field laboratory. For reasons discussed below, coral reefs are critically important marine ecosystems that should have high priority for inclusion into the LTER network. Moorea is an ideal locality for the establishment of a coral reef LTER Site.

The proposed research objectives are to better understand key processes in coral reef ecosystems that (i) modulate ecosystem function, (ii) shape community structure and diversity, and (iii) determine abundance and dynamics of constituent populations. Such mechanistic understanding will allow more accurate predictions of how coral reef ecosystems will respond to environmental change. Coordinated interdisciplinary research by our investigators (Table 1) will address the five core LTER research areas as well as themes identified as high priority for cross-site comparisons.

The science themes that form the nucleus of our research program include the: (1) biological bases for variation in ecological performance of stony corals (the foundational group); (2) population dynamics of key groups; (3) food web and nutrient dynamics; and (4) maintenance and functional consequences of diversity. Two additional research components cut across these themes: (a) an explicit focus on physical – biological coupling over multiple scales; and (b) physical and ecological models to synthesize field results and obtain generality. Identified issues within each thematic area will be explored through focused, process-oriented studies and by long-term experiments and monitoring of key abiotic conditions, ecosystem functions, and community and population attributes of major functional groups. The proposed LTER also will have strong data management and outreach components, and a commitment to involve underrepresented groups. The site will further contribute to the LTER network by providing long-term time series data on parameters common to many LTER sites and by engaging actively in cross-site comparisons.

CORAL REEF ECOSYSTEMS AND NEED FOR A CORAL REEF LTER

Despite occurring in warm, nutrient-poor waters, coral reef ecosystems rank near the top of all ecosystems with respect to annual total gross productivity and biodiversity (Muscatine & Porter 1977, Hatcher 1990, Sorokin 1990). For example, world-wide, coral reefs support ~1/3rd of all known species of marine fishes despite constituting < 1% of all benthic habitat. The large and diverse communities are supported by efficient recycling processes and by the structure provided by reef-building corals. Stony corals are the foundational group on which tens of thousands of other species rely for a variety of goods and services. In turn, the mutualism between hermatypic corals and photosynthetic zooxanthellae is the key biotic interaction underlying the ecosystem. Hermatypic corals are functionally both autotrophs (via zooxanthellae) and heterotrophs (via consumption of zooplankton) and derive carbon from multiple sources. Corals can be outcompeted by macroalgae when control by herbivores is lost. In addition to biotic interactions, numerous other biological processes (e.g., larval settlement, feeding) are influenced by a variety of abiotic events (e.g., hydrodynamics) that can operate at spatial scales ranging from < millimeter to hundreds of kilometers, and which can vary on short to long time scales. Events over the past decades have shown that coral reef ecosystems can be affected by a number of different natural and human-induced perturbations. These range from short, acute and relatively localized disturbances (e.g., storms) where return to the original state is possible to more chronic, widespread influence of shifts in climate over decades that may fundamentally alter the ecosystem (Connell 1997, Knowlton 2001).

Coral reefs are among the most complex of biological phenomena. Because of their complexity, we have an incomplete understanding of the multitude of abiotic forcing functions and biotic processes that collectively determine their structure, function and dynamics. A number of perturbations are predicted to cause sweeping change in coral reef ecosystems in the coming decades (Knowlton 2001, Gardner et al. 2003). Indeed, there are predictions that coral reef ecosystems may collapse within the coming few decades (Knowlton 2001), a period equivalent to the duration of an LTER site. While there are numerous coral reef monitoring programs (e.g., Connell 1997, Wilkinson 2002, Hodgson & Liebeler 2002), descriptive ecology alone cannot elucidate the mechanistic basis of change in these systems (Hughes & Tanner 2000).

Contemporary studies have underscored the large spatial and temporal scales necessary to attain ecologically relevant understanding of coral community dynamics (Murdock & Aronson 1999, Bellwood & Hughes 2001), and the high degree of functional connectivity among biological events operating at small scales (i.e., sub-cellular), abiotic forcing functions (e.g., light, temperature) and community dynamics. An elegant example of this is provided by coral bleaching episodes, which can only be evaluated through studies operating at landscape scales (*sensu* Mittelbach et al. 2001) and spanning years to decades. Studies of the mechanistic basis of bleaching have revealed profound connectivity among the molecular and biophysical aspects of photochemistry (Warner et al. 1999, Jones et al. 2000), the molecular genetics of the algal symbionts (LaJeunesse et al. 2003), the interactive effects of light and temperature (Hoegh-Guldberg 1999), and the bleaching pattern within and among colonies (Rowan et al. 1997). To achieve a mechanistic understanding of coral reefs, our LTER must operate at similar functional, spatial and temporal scales.

PROPOSED LTER SITE

The proposed LTER site is the coral reef complex that surrounds the island of Moorea, French Polynesia (17°30'S: 149°50'W) (Figs. 1 & 2). Moorea is a small, triangular volcanic island 20 km west of Tahiti (Fig. 2). Below we describe the site and reasons why this locality is ideal for an LTER site, particularly regarding our framework involving the dynamics of a physically forced system.

Ideal Research Setting. The coastal environments of Moorea offer an unparalleled opportunity for studies of coral reef ecosystems. An offshore barrier reef forms a system of shallow (mean depth ~ 5-7 m), narrow (~ 0.8 – 1.5 km wide) lagoons around the 60 km perimeter of Moorea (see Galzin & Pointier 1985) (Fig. 2). All major coral reef types (e.g., fringing reef, lagoon patch reefs, back reef, barrier reef and fore reef) are present and accessible by small boat (Fig. 2). The reefs are in excellent condition and have been subject to relatively few natural disturbances in the last several decades, such as *Acanthaster* outbreaks in the 1970's (Faure 1989), cyclonic storms in the early 1980's and in 1991 (Delesalle et al. 1993), and some coral bleaching (Hoegh-Guldberg & Salvat 1995). The cover of coral and abundance of reef fishes are high, and reefs in this region have not undergone a phase shift from coral to algal domination. Reef fishes have been subjected to moderately low fishing pressure, and the Territorial Government recently set aside large tracts of reefs around Moorea as protected areas (where manipulative research is allowed). Moorea also is ideal for our focus on the dynamics of a physically forced system. For example, with respect to local flow, ocean waters enter lagoons over the reef crest and exit through 3 – 5 passes in the barrier reef on each side of the island (Fig. 2); our initial flow study indicates that temporal variation in lagoonal flow speed reflects changes in the offshore wave climate (Fig. 3). Swell prevails from the southwest in the Austral winter and from the north in the summer, resulting in seasonality in exposure of different sides of Moorea to large waves and high flows.

Moorea has all of the biological features desired of a coral reef LTER site: the reef complex is circumscribed (Fig. 2), contains all major habitats and is representative of a relatively undisturbed reef ecosystem. Further, studies at Moorea easily can be placed in a regional context as it is part of the Society Archipelago and is separated from the Tuamotu Archipelago by ~ 200 km (Fig. 1). This provides ample opportunity for comparative studies within the same biogeographic setting and for studies of connectivity among populations. While reefs on Moorea are moderately undisturbed, islands in the Tuamotus are as pristine as found anywhere in the world.

Well Developed Infrastructure and Ease of Logistics. The rich research opportunities afforded by the reefs of Moorea are greatly facilitated by the existence of appropriate infrastructure and the ease with which field research can be conducted. The field portion of the proposed LTER will be staged from the Richard B. Gump South Pacific Research Station on the north shore of Moorea (Fig. 2), which has been operated by the University of California since the early 1980's (Gump.html). Station facilities include two laboratory buildings (one 'wet', one 'dry') and construction of a third laboratory building is now nearing completion. This building will contain a teaching lab, research labs, a molecular lab, library, meeting room, collection room, IT center, chemical and storage rooms, and office space. In addition, the Station has a flow-through sea water system, a dock, launch ramp, a fleet of small boats and vehicles, a Scuba compressor and dive locker. Station housing includes a dormitory and bungalows. UCSB has exclusive use of a large building that includes storage and a machine shop. The Station has a staff of 6 (director, facilities manager, administrative assistant, maintenance person, groundskeeper, housekeeper). The Gump Station has ample capacity to service the proposed LTER and is strongly supportive of our efforts (see letters of support).

The Gump Station has two important partners that will benefit greatly the proposed LTER. First, the University of California and the Territorial Government of French Polynesia have a formal cooperative agreement (document attached) that the Gump Station will assist the government through research ("with particular attention to the coral reef/lagoon system"), education and outreach. One manifestation of the agreement is the Atitia Center at the Gump Station for community outreach and education on marine and terrestrial biodiversity, traditional knowledge, and the relationship between human societies and natural ecosystems (see letter of support). The second partner is the Centre de Recherches Insulaires et Observatoire de l'Environnement (CRIOBE), part of the Ecole Pratique des Hautes Etudes (EPHE) of France. CRIOBE is located on Moorea ~ 5 km from the Gump Station and contains laboratory facilities, local reference collections and literature on the flora and fauna of French Polynesia. Numerous French scientists base their field programs from CRIOBE, including several that involve long-term monitoring (since the 1970's) of the coral reef ecosystem in French Polynesia. The Territorial Government of French Polynesia endorses the establishment of an LTER Site at Moorea (see letter of support).

Another aspect that makes an LTER site at Moorea feasible is the ease of transportation to (and within) French Polynesia, located mid-way between Los Angeles and Sydney, Australia (Fig. 1). Tahiti is serviced from the U.S. by several airlines (including *Hawaiian* and *United*), and the distance from Los Angeles is just 2200 km longer than to Honolulu. Moorea is reached from Tahiti by airplane (7 min) or ferry (30 min), and planes and boats make numerous trips per day. Our experience over the past decade has shown that we can leave UC Santa Barbara in the afternoon and be diving at Moorea by noon the following day. Moorea also has the infrastructure needed for conducting research (e.g., supermarkets, hardware stores, medical infrastructure with recompression chamber, transportation infrastructure, modern communication services).

Rich History of Research. The reefs of Moorea have been the site of much research by French scientists since the early 1970's (CRIOBE papers.html), and by U.S. scientists since the mid 1980's (Gump papers.html). Scientists at CRIOBE have been conducting long-term monitoring of aspects of coral reefs at several islands within French Polynesia since the 1970's, and Moorea is one of the locations where sampling of biota has been conducted along a permanent transect on the northwest corner of the island (e.g., Galzin 1987a, b, Payri 1987, 1988, Naim 1988, Legendre et al. 1988, Adjeroud & Salvat 1996, Adjeroud 1997, Gattuso et al. 1997, Augustin et al. 1999). In addition, some participants in this proposal have worked at Moorea since the early 1990's, and have collected time series data on fishes and corals (e.g., Fig. 5). Also, archived time series data on climate and nearshore ocean conditions are available. Our proposed work will build on this existing information.

PROPOSED RESEARCH

We envisage an LTER site at Moorea to be an interdisciplinary, decadal- and landscape-scale program that will provide a deep understanding of the processes that modulate ecosystem function, shape community structure and diversity, and determine abundance and dynamics of constituent populations. This will provide insight into the response of coral reefs to a variety of perturbations that operate across different spatial and temporal scales. The results will create the capacity to forecast the response of coral reefs to environmental conditions, thereby creating a tool to aid in the development of management strategies. To achieve this vision, we propose to: (1) conduct a monitoring program to measure decadal trends in reef biota and abiotic forcing functions, (2) undertake observations and experiments to explore processes and events affecting reef structure, function and dynamics, and (3) develop a suite of quantitative models to synthesize and generalize results. Our framework stresses integration across levels of biological organization, building from the sub-organismal to the ecosystem levels.

1. Monitoring of Long-Term Trends

The monitoring component is designed to meet the needs for comparative analyses within the LTER system, to measure long-term trends, and to provide a contextual basis for process-oriented studies. Depending on the taxon or process under investigation, the scale and scope of the monitoring will encompass a variable number of sites, zones, depths, or frequencies of sampling; Table 2 summarizes our monitoring strategy. During the first year of the award we will refine and implement the monitoring. The most spatially inclusive sampling will include three habitat types [fore reef (10 and 20 m depth), back reef, fringing reef] at two localities on each of the three shores of Moorea (Fig. 2). We will also continue the ongoing monitoring efforts we already have in place. Regional scale properties (e.g., sea-surface temperature, subsurface Chl a concentration, regional surface currents) will be estimated by remote sensing using information collected by existing satellite sensors. Biotic factors to be monitored within quadrats or along fixed transects include aspects of (i) ecosystem function (e.g., primary productivity), (ii) community-level attributes (e.g., trophic structure, diversity), (iii) population-level characteristics (e.g., abundance, dynamics), and (iv) individual-based characteristics (e.g., demography, functional metrics). In addition to climate data, abiotic factors that affect reef organisms will be monitored. Results from the first year will be used to calculate the power of the analyses in detecting temporal effects and, if necessary, the sampling regime will be revised to achieve high power for detecting changes. These analyses produce a ranking of abiotic factors based on their likely influence on biotic traits (see Menge et al. 2003), and will guide experiments to establish cause-and-effect and to provide parameter values for analytical models.

1.1. Monitoring of Abiotic Conditions

Physical Parameters. Primary physical data collection will focus on factors known to influence coral reef ecosystems: temperature, light (including UV), nutrient availability, and water flow (primarily wave-driven flow). In addition, salinity, turbidity, availability of inorganic nutrients, and the hydrographic structure and variability associated with the water column seaward of the reef sites will be monitored. Although changes in water pH that affect coral calcification due to increased atmospheric CO_2 are unlikely to be detectable over a decadal time frame (Kleypas et al. 1999), we will measure water pH periodically as part of our routine hydrographic monitoring.

Basic Sampling Design. We propose a multi-tiered array of 6 monitoring sites that correspond to the localities where biological measurements will be made. We will establish two heavily-instrumented sites on the northern shore (i.e., 2 primary sites) and two less-instrumented localities on both the eastern and western shores of the island (i.e., 4 secondary sites).

At the primary sites, water temperature will be measured continuously at 1 min intervals at 4 depths using Seabird Electronics SBE-39 (or equivalent) thermographs (0.01° C resolution) deployed 0.5 m above the bottom for up to 6 months per deployment. High frequency data collected on the north shore of Moorea in 2001-2003 (J. Leichter unpub. data) revealed a shift with depth from dominant diurnal variability associated with solar heating in the back reef and < 10 m on the fore reef, to semi-diurnal and higher frequency variability likely associated with internal tidal upwelling > 20 m on the fore reef slope. This is consistent with observations made in deeper water on the north shore of Tahiti (Wolanski & Delesalle 1995). In addition to producing temperature fluctuation of 1 to 2 °C at scales of minutes to hours, internal tidal upwelling represents a potentially important, spatially variable source of dissolved nutrients and suspended particles reaching reef slope communities (Leichter et al. 1996; 2003). Water temperatures at secondary sites will be measured with Onset Computers temperature loggers (0.2 °C resolution) at 16 min intervals.

An array of benthic instruments will be deployed at 10 m depth at both primary study sites. Multi-channel data loggers (Seabird or equivalent) will measure light (PAR), wave heights, salinity, and turbidity and be deployed for up to 6 months (light sensors cleaned bi-weekly or as dictated by fouling). Water column hydrographic profiling and collection of samples to estimate inorganic nutrient concentrations will occur weekly at the primary sites and less often at secondary sites. We will conduct a study of high frequency nutrient variability associated with internal tidal upwelling.

Seabird Electronics wave height sensors (SBE 26) will be installed at one site on each side of Moorea to sample wave spectra for 5 min per hour at a sampling frequency of 2 Hz. Depending on water depths, acoustic Doppler current profilers and current meters measuring at fixed points will record water flow within the lagoons at these same three sites over 6 month deployments. Simultaneous measurements of wave heights and currents are critical since previous studies have shown that strong flows on coral reefs and in lagoons can be driven by waves (e.g. Symonds et al. 1995; Kraines et al. 1998, Hearn 1999), including at Moorea (Fig. 3). Recording surface light meters will be placed on shore, directly inshore of all 3 sites. Oceanographic instrumentation will be complemented by collection of surface environmental data at a weather station (recording solar irradiance, atmospheric pressure, wind, temperature) at the Gump Station. Large scale observations of current and water mass variability will come from satellite remote sensing of currents (TOPEX-Poseidon, ERS, altimeter satellites), temperature (AVHRR), and ocean color (SeaWiFS, MODIS). Data on deep, ocean swell impinging on Moorea and synoptic scale meteorological variability will come from ongoing monitoring programs in French Polynesia.

Publicly available data from SeaWiFS, MODIS and AVHRR satellite sensors will be used to monitor spatial and temporal variation in such biogeophysical variables as subsurface Chl a concentration, light absorption caused by dissolved and detrital matter (Maritorena 1996, Maritorena & Guillocheau 1996, Boss & Zaneveld 2003), particulate backscattering and Sea-Surface Temperature (SST) at the scale of Moorea up to larger scales (e.g., Society Archipelago, French Polynesia, central south Pacific). Observations of large scale processes and their variations can be compared to local observations to explore links among scales. The spatial resolution of the imagery is 9 km for SeaWiFS data and 4.5 km for MODIS. SeaWiFS data have been collected since September 1997 and MODIS data since March 2000.

1.2. Monitoring of Primary Production and Controlling Factors

Net Annual Primary Production of Reef and of Reef Phytoplankton. Primary production of the reef community will be estimated using upstream-downstream respirometry (Marsh & Smith 1978). Instrument packages (CTD with O_2 sensors, flowmeters) moored on the sea floor will be used to measure changes in dissolved oxygen during the day (net community primary production) and at night (community respiration). Summed, these estimate gross community primary production. Twice-annual (summer and winter) estimates will be made over 2 day periods at all 6 sites.

Whole reef primary production is the aggregate sum of the production of the major primary producing components of the reef. Variation in whole reef production can result from changes in the relative abundances of producer components (addressed below) and/or changes in rates of metabolism of the component producers. Rates of primary production and respiration for each of the major groups (algal turfs, crustose corallines, selected macroalgae, selected corals) will be estimated using changes in dissolved oxygen in chambers/flumes under realistic conditions of light and water flow (Carpenter et al. 1991), during both summer and winter. Component rates of metabolism will be weighted by relative abundance to provide another estimate of whole reef metabolism. Vertical profiles of primary production of water column communities will be measured using standard ^{14}C tracer/bottle techniques according to JGOFS (Joint Global Ocean Flux Study) protocols (Knap et al. 1997) offshore, inshore and on the reef flat at all 6 sites. Because measure of primary production can be temporally variable, we will sample at a higher frequency (e.g., multiple times per week) for an extended period to determine the optimal sampling frequency.

Algal Community Structure. Relative abundances of the major algal functional form groups (algal turfs, crustose corallines, macroalgae) will be estimated in quadrats along established transects. Use of digital photography will be explored to make sampling as efficient as possible. Estimates of biomass (ash-free dry mass) for each of the algal components will be obtained twice annually (summer and winter) at all 6 sites. Macroalgae will be harvested in the field, returned to the lab, dried, weighed, and ashed. Biomass of algal turfs and crustose corallines will be estimated from turf and coralline covered substrata collected from the field. Algal turf canopy height (correlated with biomass) will be estimated.

Abiotic and Biotic Controls of Reef Primary Production. Concentrations of nutrients (ammonium, nitrate, phosphate, silicate) will be estimated in water samples collected when primary production is estimated. Ammonium will be measured on site using standard colorimetric methods. Other nutrient samples will be frozen and returned to UCSB for analysis. Fluxes of nutrients across reef transects will be obtained from combining estimates of cross-reef flow (meters/s), water depth (meters), and nutrient concentrations (kg/m^3) to give nutrient mass flux (kg/s/m width of reef).

Nitrogen fixing cyanophytes are a major component of most reef algal turfs. Rates of nitrogen fixation will be estimated twice annually using algal turf communities that develop on settling plates cut from coral skeletons and placed on the reef flat (Carpenter 1986). Plates will be brought to the lab and rates of nitrogen fixation estimated using the acetylene reduction technique described in Williams & Carpenter (1998). Nutrient concentrations in the environment provide discrete estimates of nutrient availability. However, growth of many primary producers is related to nutrient availability integrated over time. Estimates of integrated nutrient availability can be reflected in the

C:N and C:P ratios in the tissue of primary producers. Estimates of C:N and C:P of algal turfs and selected macroalgae will be obtained from algae collected from fore reef, reef flat, and fringing reef locations. Samples will be frozen and returned to UCSB for analysis.

Heterotrophic bacterioplankton are essential to the recovery of dissolved organic matter (DOM) and regeneration of inorganic nutrients lost from the reef community (Linley & Koop 1986, Sorokin 1994). Bacterial production estimates are elevated compared to the open ocean (Moriarty et al. 1985) and large temporal variability in bacterial production is likely linked to availability of reef DOM (Ducklow 1990). Bacterial production is elevated in interstitial spaces within the corals (Countway 1999), suggesting that corals contain regenerative spaces for nutrients (DiSalvo & Gundersen 1971). Bacterioplankton biomass (Porter and Feig 1980), production (Azam et al. 1983, Smith & Azam 1992) and DOC and DON concentrations will be monitored where and when primary production is measured. Bacterioplankton biomass and production rates will be expanded to include coral interstices, where samples will be drawn using sterile syringes. DOM remineralization experiments (Carlson et al. 2002) will assess the magnitude of available organic matter and growth efficiencies of the heterotrophic prokaryotes at offshore, above reef and reef interstitial sites.

1.3. Monitoring of Scleractinian Communities

Community Structure and Dynamics of Coral Populations. Scleractinians, macroalgae, crustose coralline algae, algal turf, and bare space will be digitally photographed and analyzed for percentage cover. Where coral cover is low, larger photo-quadrats will be used or photography will be replaced with a point-intercept method. Coral diversity indices will be calculated using species counts and colony abundances. This methodology will allow us to explore the responses of species richness and evenness to environmental change (Connell 1997, Connell et al. 1997, in press, Edmunds 2002).

To reveal mechanisms driving changes in coral cover (Hughes & Tanner 2000), coral population dynamics will be explored using a size-based demographic approach (Hughes 1984, Caswell 2001; see Fig. 6). Study species will contrast different ecologically important groups (e.g., brooders versus broadcasters). Matrix models will estimate population growth (λ) and resilience (ρ) as holistic measures of fitness (McPeek & Peckarsky 1998), and will enable us to project population structure over time (Hughes & Tanner 2000), and test for associations with abiotic conditions.

Functional Metrics of Coral "Vitality". Physiological condition of several coral species will be quantified using PAM flourometry (Warner et al. 1999, Jones et al. 1999) to assess the functionality of the zooxanthella symbionts (Warner et al. 1999, Maxwell & Johnson 2000) and detect temporal patterns associated with environmental changes. Coral recruitment will be assessed at all sites using settlement tiles (Mundy 2000) deployed annually for 6-month periods at two depths on the fore reef. Coral calcification (i.e., growth) will be assessed with a buoyant weighing approach (Davies 1989) applied to several species prepared as nubbins for transportation among depths. Short-term growth provides a phenotypic measure of fitness in corals (Bruno & Edmunds 1997), and over a long time scale, will enable us to (a) evaluate the effects of changing pCO_2 on coral growth (Kleypas et al. 1999), (b) understand the relationship between coral performance and reef accretion, and (c) interpret the seasonal growth bands within coral skeletons (Knutson et al. 1972).

In addition, we will continue to monitor annually the physical attributes of ~80 permanently marked *Porites rus* and *P. lobata* colonies along the north shore that we have been sampling since 2000 (for detail, see Holbrook et al. 2002a, b). These species represent the major patch-forming corals in lagoons of Moorea, and the colonies represent a range in size and exposure to flow.

Corals as an Archive of Past Climate Variability. Coral skeletons contain information about past climate variability in their density, fluorescent banding and isotopic and trace element content (Shen et al. 1992, Gagan et al. 2000). Because corals can be 100-200 years old, it is possible to reconstruct century-scale records of climate and environmental conditions at sub-annual resolution (Urban et al. 2000, Cobb et al. 2003, McCulloch et al. 2003) and add contextual information for contemporary monitoring of coral. We will use climate and environmental records gleaned from corals in Moorea, using established techniques, to estimate baseline climate and environmental conditions as a reference for current conditions. Coral records can help identify past bleaching events using the isotopic composition and fluorescence (Suzuki et al. 2003). Finally, the year of mortality for dead corals can be identified by matching features in coral records to known climate events.

1.4. Monitoring of Zooplankton, Reef Invertebrates and Reef Fishes

Monitoring Temporal and Spatial Variability of Zooplankton. Zooplankton abundance, biomass (dry weight and organic carbon), and community composition will be assessed along major transects at all 6 study sites day and night seasonally (2 - 3 times per year) and opportunistically throughout the year. Samples will be collected using plankton nets (333 µm mesh for macrozooplankton;100 µm for microzooplankton) in deeper waters and diver-positioned pump samplers (Sebens et al. 1992, Heidelberg et al. in press) close to the reef.

Monitoring Temporal and Spatial Variability of Reef Invertebrates. Aside from stony corals, other important meso-invertebrates on the reef will be quantified annually at the 6 study sites. Groups to be measured include coelenterates (sea anemones (e.g., Fig. 5.C)), sponges, mollusks, crustaceans (crabs), echinoderms (sea urchins, sea stars, sea cucumbers) and ascidians. Depending on abundance, these invertebrates will be sampled in quadrats or along large band transects; in addition to abundance, sizes of selected taxa will be measured. Data from intensive sampling during the first year will be used to design the sampling strategy for each invertebrate group.

Monitoring Temporal and Spatial Variability of Fish. The abundance and biomass of coral-associated fishes will be assessed along each major transect at the 6 study sites seasonally (2 - 3 times per year). Additionally, the abundance and biomass of individuals in these same functional groups occurring on a select group of focal coral heads located within each major transect site will be assessed concurrently with the larger band transects. Focal corals will be chosen to span the range of sizes, species composition, and structural morphotypes present at each site. In addition, we will continue to monitor fishes and fish habitat in lagoons of Moorea that we have sampled repeatedly for several years. These include (1) the abundance (by size class) of damselfishes sampled on permanent transects ~3 times per year since 1992 (see Fig. 5 for *Dascyllus trimaculatus*), (2) the abundances of all fishes associated with ~80 natural occurring *Porites rus* and *P. lobata* colonies along the north shore of Moorea sampled annually since 2000 (Fig. 7), and (3) all fishes on small, replicate colonies of *Pocillopora eydouxi* that were outplanted at ~15 sites around the island and sampled periodically since 1998. Finally, we will continue *daily* monitoring of larval settlement of planktivorous fishes to Gump reef from mid-June through August, which we have done annually since 1993 (Fig. 5D).

2. Research Themes and Initial Projects

2.1. The Biological Basis for Variation in Ecological Performance of Corals

This theme is motivated by the foundational role that stony corals have in the reef ecosystem, and is intended to reveal cause-and-effect relationships between abiotic conditions and coral performance. The monitoring component will provide the ecological context for manipulative experiments. In addition to field experiments, causation will be explored using shore-based "microcosms" in which corals will be grown under conditions regulated for temperature, flow, light (PAR and UV), and pCO_2; these treatments have been selected to reflect the biologically significant changes associated with global climate change (IPCC 2001). Microprocessor controlled systems will be used to control the magnitude and timing (frequency and duration) of conditions so that ecologically relevant scenarios can be investigated.

The questions appropriate for experimental analyses will evolve as the ecological context defined by empirical data is focused by the transition from an annual to a decadal perspective. However, within the first six years of this study, the following experimental analyses will be initiated:

I) How is coral larval development affected by abiotic conditions, and how does this affect dispersal, substrate selection, and ecological zonation of reef corals?

Rationale: Most reef corals produce pelagic larvae that spend short to long periods in the water column (Harrison & Wallace 1990), where they are affected by seawater conditions. Many aspects of coral larval biology currently are under investigation (Ball et al. 2002), yet despite strong evidence of the detrimental effects of high temperature on coral reproduction (Szmant & Gassman 1990, Omori et al. 2001, Bassim & Sammarco 2003), little is known concerning the response of coral larvae to effects of climate change. It is likely that dispersal of coral larvae and the density of spat may be altered (Edmunds et al. 2001), and recent work from the Virgin Islands implicates thermal effects in mediating the dynamics of juvenile corals (Edmunds in press). Because coral larvae are not equal within a brood (Edmunds et al. 2001, Isomura & Nishihira 2001), fluctuating abiotic conditions could determine which larvae are successful.

Approach: The approach will be to incubate larvae in a factorial experimental design and assess their response using variables that allow for an interpretation in an ecologically relevant context. The initial experiment will focus on larvae from brooding species (e.g., *Pocillopora* spp.) because of the ease of access, but later experiments will use spawning species (e.g., *Acropora* spp.) after techniques are proven. Pertinent experiments will address: (a) the interactive effects of temperature and age on larval metabolism, zooxanthellae composition, longevity and settlement choice (Fig. 8), (b) the interactive effects of temperature and pCO_2 on larval success, and (c) the effect of treatment conditions on gene expression.

*II) (**A**) How are the physiology and symbiotic status of corals affected by the magnitude and temporal structure of abiotic fluctuations, and (**B**) what are the gene-expression events that transduce abiotic conditions to organismic responses with ecologically significant ramifications?*

Rationale: Corals are recognized as marine organisms living in physically heterogeneous habitats, which in the case of at least one abiotic trait (temperature) maintains them near the upper limits of their tolerance. Although some performance of the coral may be plastic due to potential shifts in endosymbiont types with varying abiotic conditions (e.g., the Adaptive Bleaching Hypothesis; Buddemeier & Fautin 1993, Baker 2002), there is not a clear understanding of how the prevailing conditions influence the performance of the coral, and whether they have sufficiently plastic physiology to adjust to changing conditions. One important manifestation of this problem is a lack of mechanistic information concerning whether (or not) reef corals will (or can) acclimatize to the changing conditions associated with global warming (Gates & Edmunds 1999). Despite early concern that corals might die before they could adapt (Hoegh-Guldberg 1999), there now is evidence that some corals have acclimated to warmer conditions (Berkelmans et al. 1999, Brown et al. 2001), and that future reefs will have different assemblages, but will not be absent (Hughes et al. 2003).

Manipulative experiments will test the response of a variety of coral species to different environmental conditions in order to better understand: (a) the organismic basis of the response, and (b) the mechanisms driving shifts in community structure (e.g., why species differ in susceptibility to environmental degradation). There are significant gaps in our understanding of how corals translate physical signal into physiological response, and how the benefits and costs of that response manifest themselves at the organismal and population scale. For example, in the case of heat stress, previous research has shown that corals do respond predictably to heat stress in the lab: the next step in these investigations is to use emerging molecular techniques such as DNA microarrays to dissect the response of the coral to a thermal signal and determine what genes and metabolic processes are being activated in response to variation of multiple physical factors in the water column.

Approach: A two-fold approach will employ lab and field experimentation (Fig. 6). First, corals will be incubated under a range of conditions and their responses assessed as: (a) dark respiration and gross photosynthesis (both as oxygen flux), and (b) changes in zooxanthellae clades (LaJeunesse et al. 2003). The experimental conditions will be manipulated to test perturbations of magnitude and timing as well as the effects of initial stressors on future responses [i.e., to tease apart the effect of history (*sensu* Brown et al. 2001) on future responses]. Second, the monitoring component of the LTER project will be used to identify sites with differing abiotic regimes but broadly similar coral species assemblages. To test whether the geographic distribution of host/symbiont combined genotypes reflects the magnitude of the environmental range found in a given habitat, we will define the host and symbiont genotypes of three corals - *Montipora spp.*, *Porites lobata*, *Pocillopora damicornis*. Gates' lab at HIMB already is funded to develop microsatellite markers with population level resolution for these taxa in Hawaii. A subpopulation of each of the study species will be reciprocally transplanted among sites and the impact of changes in environment evaluated by comparison with control (undisturbed) controls and corals that are routinely assessed in monitoring research. Response variables will be assessed post-transplantation and bi-annually thereafter as follows: (a) survival and photosynthetic capacity (described above), (b) symbiont types, (c) activity of key metabolic processes, and (d) expression of environmentally responsive genes. It is critical that these metrics are assessed for at least six years as it is uncertain what time scale is ecologically relevant to changes in zooxanthellae types. To evaluate symbiont genotypes, symbionts will be isolated from the coral and analyzed to describe the microsatellite and ITS2 type. These data, collected over a period of years to decades, will test the adaptive bleaching hypothesis (Buddemeier & Fautin 1993). The activity of key metabolic processes will be evaluated using monoclonal antibodies currently being raised (at HIMB) against proteins that are involved in environmental regulation and the amelioration of stress in corals. These antibodies will be used in

ELISA assays to evaluate the activities of each of the proteins in the sampled coral tissue to provide important details regarding the metabolic "health" of the symbioses. Expression of environmentally responsive genes will be evaluated using DNA microarrays currently under development (at HIMB and UCSB), and we plan to use them to examine the temporal expression of environmentally responsive genes in several coral species. Additionally, corals from the microcosm experiments and monitoring program will be sampled for assessment of single-candidate genes that are activated by stress using Northern analysis and real-time PCR (Buckley & Hofmann 2003).

2.2. Population Dynamics

The general aim is to elucidate the processes that determine local dynamics of key constituents of coral reef ecosystems. Our initial focus will be on stony corals and coral-associated fishes, but later we will include other important groups (e.g., algae, invertebrates; Table 2). We seek to understand the role of differences in key life history attributes, to identify major sources of variation and life history phase(s) where regulation occurs, and to quantify the nature, magnitudes and causes of post-settlement losses. Connectivity among populations will be explored to better understand the link between local processes that influence fecundity and local and meta-population dynamics. For species with dispersing propagules, local dynamics are shaped by the input rate of young and subsequent density-independent and density-dependent losses (Doherty & Fowler 1994, Caley et al. 1996). Input is affected by the flux of larvae, which is the product of larval concentration and flow speed (Gaines & Bertness 1993). Larval concentration depends on reproductive output and processes that influence subsequent losses and introduce spatial patchiness (Gaines et al. 1985, Kingsford 1990, Hughes et al. 2000), whereas settlement involves an interplay between the attributes of a specific locality (e.g., appropriate habitat or cues) and the biology of a larva (Raimondi & Morse 2000, Kingsford et al. 2002, Almany 2003). Performance after settlement is shaped by abiotic and biotic factors, which can co-vary with processes influencing input (Shima 2002, Shima & Osenberg 2003). Like for fishes (Brunton & Booth 2003), mortality of corals is size–dependent (Hughes 1984). The per capita effects of these influences may or may not scale with population density (Forrester & Steele 2000, Osenberg et al. 2002). Local effects on fecundity may not be expressed locally as reproductive output often is exported from the natal reef (Lecchini & Galzin 2003), although downstream effects can be important (Chesson 1998, Armsworth 2002).

Progress in resolving a long-standing debate regarding the importance of these various processes to dynamics of reef fish populations sharpens our understanding of major issues that remain unanswered. The genesis of the dispute is the failure to detect density-dependence in post-settlement mortality in numerous studies and the finding of (argued to be strong) density-dependence in numerous others (reviews by Hixon & Webster 2002, Osenberg et al. 2002). These conflicting findings resulted in controversy regarding when regulatory processes operate in the life cycle of reef fishes. We recently undertook a meta-analysis of empirical data from 71 studies, which revealed - contrary to conventional wisdom at the time - that the *per capita effect of density on mortality* (β) **was not different** on average between studies where density-dependence was detected and those where it was not (Osenberg et al. 2002). What did differ was the *total effect of density on mortality* (βN), reflecting a higher average ambient population density (N) in systems where density-dependence was detected. Further, there was substantial heterogeneity in β regardless of the author's conclusion regarding density-dependence (Osenberg et al. 2002). These results indicate that future explorations should address: (1) why different systems exist at different densities, and (2) what causes variation in per capita strength of density-dependence. These issues form our initial foci.

A. Studies on Dynamics of Corals

I) Is there a relationship between local coral fecundity and settlement and how does it vary across spatial scales and among species with different life history attributes?

Rationale: Hughes et al. (2000) used a hierarchical sampling scheme to explore the relationship between adult density, fecundity and recruitment of Acroporid corals along the Great Barrier Reef. Spatial and temporal variation in fecundity of the most common species of *Acropora* explained 72% of the spatial and temporal variation in larval recruitment, indicating that production of larvae was a major determinant of recruitment levels, at least at larger scales (Hughes et al. 2000). The strength of such stock-recruitment relationships may vary with life history of corals (e.g., brooders vs. free-spawners) and across spatial or temporal scales. The extent to which local recruitment is linked to local fecundity suggests that sublethal changes in fecundity could greatly influence local dynamics.

Approach: We will adopt the same methods used by Hughes et al. (2000) to explore this issue at Moorea for a variety of common corals that represent different reproductive modes. Initially, the spatial hierarchy of sampling will be (from largest to smallest) the whole island (inter-annual patterns only), the three sides of Moorea, three equal sections within each side, and replicate transects (500 m^2) within each section. Sampling of fecundity will occur just prior to the initiation of the major spawning period, and sampling of new recruits (on standardized panels) will be estimated for the subsequent 3 month period.

II) How are growth and survivorship of new coral recruits affected separately and jointly by variation in flow and corallivory, and how do coral attributes influence these effects?

Rationale: Mortality rates of corals are highly size-dependent with the greatest risk of mortality occurring in the period after settlement (Hughes 1984). Among the factors known to have major influences on juvenile coral growth and survivorship are current flow (which affects food and nutrient supply, and sedimentation rates) and biotic interactions (Grottoli-Everett & Wellington 1997, Lourey et al. 2000, Edmunds & Carpenter 2001) (Figs. 9 & 10). Work in other marine systems has shown that flow and predation can interact in complex ways to control the population dynamics (Lenihan et al. 2001) and community composition of sessile invertebrates (Leonard et al. 1998). For example, flow can enhance growth rates thereby increasing survivorship through provision of size refuges (Lenihan 1999), or alter the abundance or effectiveness of predators (Leonard et al. 1998). How flow and predation interact to influence demographic rates of coral species has yet to be adequately explored. Different types of corals are likely to be affected differently by the same variation in these factors, but as yet, we lack a full understanding of the joint effects of flow and predators relative to coral attributes.

Approach: In addition to surveys, we will conduct field experiments to estimate the separate and joint effects of current flow and predation on growth and survivorship of juvenile corals. We have developed techniques to influence local flow speeds (experimental reefs) and predator abundances (predator exclusion cages), and preliminary results are promising (Figs. 9 & 10), suggesting that growth and survivorship of different species of corals do indeed respond differently to the same variation in flow. The experiment will be conducted at several sites selected to represent a range in ambient flows and abundance of corallivores (butterflyfish, parrotfish, Muricid gastropods); at each locality, experimental reefs will be constructed that alter localized flow speeds; the structures result in three localized flow treatments within a site. Small colonies (5 and 20 mm diameter) of four common coral species (*Pocillopora eydouxi, Acropora elseyi, Porites lobata, P. rus*) will be outplanted and subsequent growth and survivorship estimated for a minimum of three years. Sedimentation, flow, and corallivore abundances will be estimated. In addition, at selected locations, we will reduce the abundance of corallivores by surrounding randomly selected, outplanted corals with predator exclusion cages or cage controls. Our preliminary experiment (Fig. 10) indicates that with modest maintenance, cages can exclude corallivores with little influence on flow.

B. Studies of Dynamics of Reef Fishes

I) What are the source populations of larval recruits of reef fishes at Moorea?

Rationale: One largely unanswered question is the natal source of recruits to a given reef. Pelagic larval stages are capable of dispersing long distances (Bernardi et al. 2001, 2003), and the extent of and spatial scales over which local populations are connected via larval dispersal is unknown (Jones et al. 1999, Cowen et al. 2000, Mora & Sale 2002). Among other reasons, this is an important issue because dispersal modifies the dynamical effect of local reproduction, and there is growing evidence that local retention of larvae may be more widespread than previously believed (Jones et al. 1999, Swearer et al. 1999). We will begin to explore where settled larvae were produced.

Approach: Several different techniques have been used to estimate sources of local recruits, including marking (Jones et al. 1999), elemental finger-printing (Swearer et al. 1999) and genetic markers (Bernardi et al. 2003). Our initial approach will be to further elaborate a genetic marker approach by developing microsatellites that potentially can identify the maternal source, coupled with an understanding of current flows on larger spatial scales. With the advent of DNA sequencing, the search for rapidly evolving nuclear regions (appropriate for ecologically relevant scales) focused on non-coding regions such as introns (Palumbi & Baker 1994, Schlee et al. 1996, Quattro & Jones 1999), Internally Transcribed Spacers (ITS1 and ITS2) (Phillips et al. 1992, Vogler & DeSalle 1994), anonymous single copy nuclear markers (Karl & Avise 1993), coding regions (Bernardi et al. 1993, Burton & Lee 1994), random amplified regions (RAPDs) (Sultman et al. 1995), and microsatellites (Wright 1993, Rico et al. 1996, Wimberger et al. 1999). In recent years, power has been best obtained by using a combination of fast-evolving nuclear markers. For this project, we will use a combination of microsatellite markers, as well as SNPs (single nucleotide polymorphisms). We will use two groups of microsatellite primers: specific primers developed in the laboratory for a few target species, as well as universal fish microsatellite primers (e.g., Rico et al. 1996, Zardoya et al. 1996). In addition to an initial focus on planktivorous damselfishes, we eventually will apply this approach to many species of fishes at Moorea; the use of "universal" primer pairs is an efficient way to obtain quickly results with a large number of acanthopterygian species (Rico et al. 1996). These primers work particularly well with the species we are planning to work with initially (e.g., primer TmoM27; Zardoya et al. 1996). Single nucleotide polymorphisms are a powerful method to score large numbers of rapidly evolving polymorphisms. We will use a method that rapidly identifies hundreds of SNPs in non-model organisms (Buetow et al. 2001).

II) (***A***) *How much temporal variation in settlement of reef fishes can be explained by variation in production and hydrodynamics and (**B**) how do local-scale hydrodynamics interact with larval capabilities to influence spatial patterns of settlement of reef fishes?*

Rationale: Understanding the causes of temporal variability in settlement is another major challenge being explored by population ecologists working on marine animals. Similar to most reef fishes examined to date, we have found the magnitude of larval settlement of several closely related damselfishes at Moorea differed greatly among settlement pulses and among years. Further, even closely related species can show markedly different spatial patterns of concurrent settlement (Schmitt & Holbrook 1999a, 1999b, 2002a). In general, we do not understand the causes of this variation among species, although it may be related to differences in larval responses to variation in nearfield flow speeds (Fig. 4) (Schmitt & Holbrook 2002b).

Approach: Our initial approach to exploring causes of temporal variation in settlement will be correlative and will use damselfishes as the model system. We first will explore how much temporal variation among settlement pulses can be accounted for by variation in larval production, in physical processes that transport newly hatched larvae offshore, in offshore oceanographic conditions during development, and in physical processes that transport competent larvae back to the reef. As part of the monitoring program, settlement of damselfishes will be estimated daily from June to September each year (the annual peak: Schmitt & Holbrook 1999b). Production will be estimated at several localities in the lagoons along the north shore of Moorea. This will be facilitated by the fact that damselfishes breed synchronously at discrete locations and times and deposit egg masses on particular benthic surfaces; larvae hatch from eggs after a few days and are transported out of the lagoon by currents that flow through passes in the barrier reef. We will estimate temporal variation in production (among reproductive cycles) by estimating the number of breeding pairs, eggs produced (by sampling egg masses), and newly hatched larvae (using quantitative net tows as larvae are transported through passes). Current speeds and offshore wave climate will be measured continuously throughout the 28 day reproductive cycle of damselfishes. Multivariate techniques will estimate the amount of variation in settlement among events that can be explained collectively and separately by the independent variables; results will guide development of experiments to test causation should strong relationships emerge.

With respect to spatial variation in settlement, we will explore the relationship between nearfield flow speeds and settlement for fishes in a manner similar to that done by us for *Dascyllus* (Fig. 4) (Schmitt & Holbrook 2002b). In brief, we will establish a series of permanent sites (~10) in close proximity along the north shore (to minimize spatial variation in larval concentrations) that differ in average flow speeds, add a standardized amount of suitable habitat for fishes, and monitor natural settlement of species among several settlement pulses. Additional sites will then be selected based on models of current flow within the lagoon to test relationships established at the original locations. In addition, we will design flume studies where individual larvae (captured by light traps prior to settlement) are exposed to a variety of flow speeds typical of the lagoons of Moorea to further explore the relationship between flow speed and ability to settle.

*III) (**A**) What causes variation in the strength of density-dependent mortality, and (**B**) how do hydrodynamics influence the strength of density-dependent growth in reef fishes?*

Rationale: Our meta-analysis (Osenberg et al. 2002) indicated that a critical, unanswered issue was the causes of variation in the per capita strength of density-dependent losses. For reef fishes, density-dependent mortality appears to be greatest during the juvenile phase and largely results from predation (Hixon & Webster 2002). For example, for the *Dascyllus* system in Moorea, overall mortality rates of juveniles varied substantially among sites, but the spatial pattern of mortality was temporally consistent and well predicted by variation in predator densities, which in turn were strongly associated with variation in shelter / ambush space for predators (Holbrook & Schmitt 2003). Further, we understand well the mechanism that results in density-dependent mortality of juvenile *Dascyllus* (Holbrook & Schmitt 2002), which involves an interaction between competition for shelter space by juveniles and predation. Our initial study will explore the causes of variation in density-dependent per capita mortality (β) in the *Dascyllus* system, then will be expanded to explore other species and causes in variation in identified causal agents (e.g., predator densities).

Habitat quality (e.g., predator density, food flux) varies spatially, and when habitat quality and settlement co-vary, density dependence can be masked if the relationship is positive (i.e., cryptic density-dependence; Shima & Osenberg 2003) or can be misinterpreted as overly strong if quality and settlement are negatively correlated ('apparent' density-dependence). Osenberg, Bolker and St. Mary from the U. Florida are funded by NSF to explore issues related to cryptic density-dependent mortality of reef fishes at our proposed LTER site at Moorea, and we propose to complement their efforts by exploring possible relationships between current flow and density-dependence in growth of planktivorous fishes. Flow not only delivers larvae, it also delivers food for planktivorous fishes and the corals that shelter them. Density-dependent growth, often reported for planktivorous fishes, can result from food limitation (Jones 1987a, 1987b, Forrester 1990).

Approach: We will use an experimental approach, using well proven techniques developed for this system, to explore the causes of variation in per capita effects of density on mortality. We will establish several study sites that vary in structural aspects suspected of influencing densities of predators, and transplant the same amount of suitable settlement habitat for damselfishes. We will mimic temporal variation in settlement that is spatially uniform by capturing newly settled damselfishes and transplanting them to each site; the same number of juveniles will be outplanted for each trial, but the number will differ among trials (from 1 to 15 per coral head, with multiple temporal replicates of each treatment) to obtain temporal variation in initial densities. The number of juveniles that survive after 48 hrs will be estimated for each trial. These data will enable us to estimate separately spatial variation in the density-dependent (β) and density-independent (α) components of mortality using techniques we previously have developed (Schmitt et al. 1999, Osenberg et al. 2002). Variation in β and α will be correlated with variation in predator densities and structural aspects of the reef. Results will guide development of further experiments to explore causation (e.g., manipulate predator densities, shelter for predators). The initial experiments will be repeated at the same sites using young of different fishes to explore generality.

With respect to the effect of flow on growth of damselfishes, a field experiment will be conducted where standard amounts of coral (heads of *Pocillopora eydouxi*) will be outplanted at a number of sites (6-8) with different characteristic flows (initially predator density and reef structure will be held constant). The density of newly settled *Dascyllus flavicaudus* and subsequently *D. aruanus* will be manipulated to achieve variation in fish density within a site; several density treatments (e.g., 2, 4, 8, 16; replicated among corals) will be established at each site. Focal individuals will be marked (subcutaneous tattoos) and additional settlers removed to maintain treatments. Body growth and survivorship of the focal cohorts will be estimated for up to a year, after which the fastest growing survivors will have reached maturity. We will estimate density-dependence in growth and survivorship for each site, and determine the extent to which these parameters are correlated with variation in flow speeds (measured continuously throughout the experiment) among the sites. Depending on initial results, a subsequent food addition experiment will be designed to test the food limitation hypothesis using methods developed by Forrester (1990).

2.3. Food Web and Nutrient Dynamics

There is still considerable debate about the relative importance of nutrient and light limitation in the control of reef primary production (Barnes & Devereux 1984, Larkum & Koop 1996, Szmant 1996), the degree to which reefs are closed or open systems (Atkinson 1987, Smith & Kinsey 1988), and the relative importance of bottom-up processes versus the top-down control of primary producer abundance (Hatcher 1996), especially regarding causes of shifts from coral to algal domination (Hughes 1994, Lapointe 1997, Hughes et al. 1999). Higher trophic levels (herbivorous fishes) also may be controlled by bottom-up forces (Russ 1984, 2003).

The major groups of primary producers on coral reefs are scleractinian corals, other zooxanthellae-containing invertebrates, macroalgae, algal turfs, and free-living algae that form a thin veneer over dead coral (Marsh 1976, Carpenter 1986). Algal turf communities (Hatcher 1982) are generally < 1 cm tall but contain up to five algal divisions (Scott & Russ 1987, Hackney et al. 1989). Rates of photosynthesis of algal turfs are affected by light (Carpenter 1985), water motion (Carpenter et al. 1991, Carpenter & Williams 1993), and nutrient concentrations (Williams & Carpenter 1988). In shallow water light is not limiting except in areas of very high spatial heterogeneity (Adey & Steneck 1985). Rates of nitrogen fixation also are enhanced by water motion (Carpenter et al. 1991, Williams & Carpenter 1998). Metabolic and nutrient uptake processes of other organisms also can be related positively to flow (Patterson et al. 1991, Atkinson & Bilger 1992, Bilger & Atkinson 1992, Atkinson et al. 2001). At small scales (cm to meters), boundary layer dynamics and mass transfer of materials to and from surfaces are critical in modulating rates of material exchange and metabolism.

Nutrients (primarily N and P) are generally considered limiting on coral reefs, largely because they are present in low concentrations. However, it is the flux of nutrients that is important for maintaining primary production (Atkinson 1987). While historical emphasis on nutrient recycling processes has led to the paradigm that coral reefs are closed ecosystems (Smith & Kinsey 1988), recent approaches reveal the modulation of nutrient uptake (and presumably nutrient status) by water motion and boundary layer dynamics (Atkinson & Bilger 1992, Hearn et al. 2001) The connection between nutrient delivery and uptake and oceanographic-scale processes (e.g., wave height) suggests that coral reefs are much more open communities in this context. Moreover, how changes in flow-mediated primary productivity cascade to other trophic levels remains unknown.

Recent studies have also suggested that the apparent paradox of high primary productivity in apparently nutrient poor waters could be explained by rapid and efficient microbial processing of the large amounts of organic matter released by reef heterotrophs, giving rise to high rates of nutrient flux through the detrital component of the food web (Atkinson 1987, Sorokin 1990). Yet little is known about the mechanisms or key players controlling the movement rates of nutrients within it (Arias-Gonzalez et al. 1997). Bacterial production is elevated in interstitial spaces within the corals (Countway 1999), suggesting that corals contain regenerative spaces for nutrients (DiSalvo & Gundersen 1971). Moreover, despite similar abundances, bacterial production is often greater over reefs than in the open ocean (Ducklow 1990, Countway 1999), indicating that removal processes differ considerably between the two systems. Removal by corals and other reef invertebrates may play a major role in cropping bacterial biomass (Sorokin 1978, Ducklow 1990).

As functional autotrophs, hermatypic corals are important reef primary producers. Nutrient availability to corals is controlled by ambient concentrations in the surrounding water, water motion, and boundary layer dynamics (Atkinson & Bilger 1992, Hearn et al. 2001). Nitrogenous wastes and feces released by fishes sheltering in branching corals may augment ambient nutrient concentrations in the waters immediately surrounding these corals (Arias-Gonzalez et al. 1997, Depczynski & Bellwood 2003). This pathway shunts nutrients in the pelagic and demersal component of the reef food web to corals. As consumers of zooplankton and other invertebrates, hermatypic corals also play a role in heterotrophic pathways within coral reef food webs. Growth rates of corals increase with increasing consumption of zooplankton (Leichter et al. 1998, Ferrier-Pages et al. 2003) and certain aspects of coral growth morphology and polyp characteristics may represent adaptations for zooplankton capture (Sebens et al. 1997). Moreover, along this pathway, schools of sheltering zooplanktivorous fishes may compete with corals for zooplankton and thus it is unclear whether such fishes resident in corals provide a positive or negative net benefit to their hosts. A full understanding of the contributions of zooplankton and planktivorous fishes to the supply of carbon and nutrients required by hermatypic corals is needed to predict how environmental stressors (e.g., increased temperatures leading to bleaching, increased nutrient loading, changes in abundance of fishes) may alter pathways of carbon and nutrient input to corals.

A. Process-oriented Studies on Coral Reef Trophodynamics

I) How do local-scale hydrodynamics interact with reef morphology to determine benthic community structure and primary production?

Rationale: High water flow can be a source of disturbance to reef communities, opening space on the benthos and initiating successional changes in the community. Breakage and dislodgment of reef organisms can induce changes in morphology that alter small-scale flow patterns around the organism affecting exchange of gases and nutrients, particle capture and metabolism. Uptake of nutrients and other compounds are controlled by boundary layer development and disruption which are a function of flow dynamics. To understand controls and limits on gross primary production and explain its substantial spatial and temporal variation, we need to elucidate the coupling between local hydrodynamics, reef morphology and roughness, and primary production (Fig. 11).
Approach: Our initial exploration of effects of hydrodynamics will use a correlation approach. We will quantify water movement at several spatial scales (regional, local, reef, organismal), reef morphology/roughness, and rates of primary production across a range of hydrodynamic conditions. The three coasts of Moorea experience very different hydrodynamic conditions and the study sites established along each coast will serve as the foci for these studies. Regional-scale hydrodynamic conditions will be quantified as part of the monitoring effort. Reef-scale water movement will be measured at each site and wave heights will be measured using bottom-mounted pressure sensors on both the shallow fore reef and back reef. Wave energy flux will be estimated from wave height estimates and root mean square flowspeeds as measured by ADVs and ADCPs. Estimates of primary production of shallow reef flat/back reef communities will be coupled with the hydrodynamic measurements. Primary production will be measured using upstream-downstream respirometry (Marsh & Smith 1978) using bottom-mounted instrument packages. Estimates of surface roughness and benthic community composition will be obtained for each transect/time combination. Experiments will be devised to explore causation if significant correlations arise in our analyses.

II) To what extent are coral reef primary consumers regulated by the cascading effects of bottom-up control due to hydrodynamic modulation of reef primary production?
Rationale: Several lines of evidence suggest that coral reef primary consumers are regulated in part by the availability of algal resources. Primary consumers are more abundant in shallow, well-lit zones where rates of primary production are highest (Hatcher 1988). Removal of competitors either experimentally (Hay & Taylor 1985) or from disease (Carpenter 1990) resulted in functional and numerical responses by some herbivorous fishes to increased algal availability. Herbivorous fishes were more abundant on outer shelf reefs of the GBR and abundance was correlated positively with the production (turnover) of algal resources (Russ 1984, 2003). Combined with the recent demonstration that algal turf primary production (the primary food for herbivores) is modulated by water flow and mass transfer processes (Carpenter et al. 1991, Larkum et al. 2003), it is likely that primary consumers are regulated in a trophic cascade driven from the bottom by hydrodynamic forcing. Water flow also influences local abundances and feeding effectiveness of primary consumers by determining conditions under which herbivores can forage.
Approach: Following quantification of the relationship between water flow and primary production (above), secondary production of major primary consumer species will be estimated among sites that vary in primary production. Secondary production will be estimated from size-abundance estimates and size-biomass relationships. Shorter-term functional responses of primary consumers to resource availability will be quantified by estimating foraging time, bite frequency, and grazing area (using video analysis) as a function of primary production and hydrodynamic conditions.

III) What are the long-term interactive effects of herbivory and nutrient availability on coral reef benthic community structure and function?
Rationale: Primary space on coral reefs is dominated by free-living algae (algal turfs, macroalgae, crustose corallines) and symbiont-containing invertebrates whose relative abundance is determined to a great extent by two opposing processes. Nutrient (primarily nitrogen and phosphorus) availability promotes growth of algae and may give them a competitive advantage over corals (Littler et al. 1992). Herbivory reduces algal abundance and keeps reefs dominated by diminutive algal turfs and crustose corallines, promoting coral abundance (Steneck 1988). The shift in benthic community structure on many coral reefs from coral/algal turf domination to macroalgal domination (phase shifts) has renewed interest in the roles of nutrients and herbivores in maintaining reef community structure and function. An emerging understanding is that under the oligotrophic nutrient conditions typical of most coral reef environments, herbivory limits the biomass accumulation of algae and keeps the algal community dominated by species that either are capable of regrowing quickly (algal

turf species) in response to grazing, or by crustose corallines that are able to resist grazing (Steneck 1988). Simultaneous manipulation of herbivory and nutrient availability indicates that nutrients have an important effect only when herbivory is reduced (Miller et al. 1999, Jompa & McCook 2002). However, nutrient availability has been represented by water column concentration when it should be represented as nutrient flux that is a function of water flow past organisms and communities. The long time period afforded by an LTER will allow tests of effects of herbivory and nutrient flux across sites that vary in hydrodynamic conditions.
Approach: Gradients in flow and nutrient concentrations (from low to high) typically occur from nearshore fringing reefs to the outer barrier reef; these gradients combine to produce variation in nutrient flux. These conditions will be exploited to establish experimental manipulations of herbivory that allow different combinations of nutrient flux and herbivore access (primarily echinoids and herbivorous fishes). Response variables will be algal community structure, biomass of each algal component, and rates of primary production. Importantly, these relationships will be quantified over multi-year periods to assess their temporal constancy.

B. Studies on Coral – Plankton – Planktivore – Predator Interactions

*I) (**A**) How do abundance and composition of zooplankton actually available to corals and fishes change on various spatial and temporal scales, and (**B**) which zooplankton sources (oceanic, demersal, resident holoplankton, meroplankton) are most critical for food web functioning?*

Rationale: While zooplankton on reefs have many sources (newly arrived and resident holoplankton, demersal zooplankton emerging from the reef at night, episodically released meroplankton), the individuals directly contacting corals or entering the feeding sphere of planktivorous fishes are the most important for food-web dynamics on the reef. In general, densities and biomass of zooplankton over French Polynesian reefs are 1 - 2 orders of magnitude greater at night (Table 3), due both to emergence and vertical migration of resident forms and to the higher nocturnal abundance of zooplankton entering the reef from the surrounding ocean (Sorokin 1991, Renon 1977, 1978, Carleton & Doherty 1998). Less is known about microplankton on French Polynesian reefs although food web models suggest that protozoan contribution to carbon cycling is small (Niquil et al. 1998). While monitoring will provide a general assessment of temporal and spatial variability of zooplankton, food-web studies will focus on highly local scales.
Approach: The diversity of behaviors and many sources of reef-associated zooplankton make sampling methodology challenging (Sorokin 1991, Heidelberg et al. 1997). We will assess the abundance and composition of micro and macrozooplankton in the vicinity of targeted corals and fish assemblages over a variety of temporal scales (day, night, dusk, lunar) using pump samplers, successfully used previously for near-reef studies (after Sebens et al. 1992; Heidelberg et al. in press). These will be positioned by divers at distances above the reef relevant to planktivorous feeders. Pump samplers yield considerably higher zooplankton concentrations then nets. Emergence traps (Alldredge & King 1977, 1980, 1985) and nets will also be deployed at targeted sites to better identify sources of these near-reef zooplankton. Prey abundance will be determined in concert with coral and fish feeding studies. Current velocities and directions will be determined simultaneously with an Acoustic Doppler Velocimeter (ADV) to assess delivery rates of drifting zooplankton at various distances above the reef. Highly heterogeneous distributions in the wake of coral heads and at varying distances from coral surfaces are expected. Zooplankton behavior and predator avoidance will be assessed from patterns of distribution around corals and by observation of the escape responses of major zooplankton species filmed in aquaria at the Gump station and in the lagoons using infrared video (Holbrook & Schmitt 1999, 2003).

(II) What is the relative importance of direct and indirect effects of planktivorous fishes on the supply of carbon and nutrients available to hermatypic corals?

Rationale: Colonies of several families of branching corals common at Moorea provide shelter for numerous species of reef-associated fishes. Fish abundance and species richness on these corals are related to the species, size, and morphology of the individual coral colony such that larger, more structurally complex corals have higher abundances and species richness values for fishes (Holbrook et al. 2002b). In return, fishes sheltering or residing in corals release nitrogenous wastes and defecate over corals, increasing ambient levels of nutrients near their coral hosts (Arias-Gonzalez et al. 1997, Depczynski & Bellwood 2003). This positive feedback loop whereby larger, more structurally complex corals host larger populations of fishes which then provide greater inputs of nutrients increasing coral growth rates potentially may be offset by the direct negative effects resulting from competition between resident zooplanktivorous fishes and coral polyps for zooplankton.

Large, demersal zooplankton, a major form of zooplankton consumed by corals (Porter 1974, Sebens et al. 1996), are more abundant at night in Moorea (Table 3). In addition to reducing predation pressure, nocturnal feeding by coral polyps may represent temporal partitioning of the zooplankton resources with diurnal planktivorous fishes that concentrate on species of oceanic and reef associated holoplankton. Mutualistic and competitive relationships between corals and zooplanktivorous fishes may be further mediated by the presence of resident and mobile predators [e.g., hawkfishes, jacks, sandperches, wrasses]. We found that hawkfishes on *Pocillopora eydouxi* reduced abundances of damselfishes and inhibited larval recruitment (Fig. 12). We found large mobile predators such as jacks increased the amount of time zooplanktivorous damselfishes spent sheltering in coral and thereby, may increase inputs of waste-derived nutrients from fishes to corals.

Approach: Estimating the net effect of zooplanktivorous fishes on performance of hermatypic corals initially will involve correlation studies of fish and coral feeding rates in the field, abundances of the major zooplankton species in the water and in the diet, and relationships between coral size and structural complexity, abundances and growth rates of zooplanktivorous fishes, and growth rates of corals along the three coasts of Moorea (which experience different hydrodynamic conditions). Fish and coral feeding rates will be observed by divers during the day and through the use of infrared video cameras at night (Holbrook & Schmitt 1997, 1999, 2002). Zooplankton abundances in the water surrounding randomly chosen, focal coral heads will be sampled in the manner described above for studies of zooplankton. Consumption of zooplankton by corals will be estimated from *in situ* flow speeds and zooplankton abundance, and capture rates / efficiencies measured in laboratory experiments. Consumption of zooplankton by fishes will be estimated from gut contents of individuals captured immediately after cessation of crepuscular feeding and from laboratory feeding experiments. Abundances of zooplanktivorous fishes on focal coral heads will be estimated using diver surveys. Growth rates of corals and fishes will be determined by using methods described above for corals and examination of daily otolith growth increments for fishes.

Following these initial studies, we will conduct field experiments using replicate colonies of *Pocillopora eydouxi* outplanted at sites along the three shores of Moorea. This coral is fast growing, easy to outplant, and hosts large colonies of zooplanktivorous fishes (Schmitt & Holbrook 1999c, 2000). Corals will be marked to determine growth rates, and assigned randomly to treatments where zooplankton availability, abundance of zooplanktivorous fishes, and presence or absence of predators are varied orthogonally. We will use techniques of Sebens et al. (1998) to manipulate the amount of zooplankton available to corals in the field, and we have experience manipulating and maintaining densities of the zooplanktivorous and predatory fishes (Schmitt & Holbrook 1999a, 2000, Holbrook & Schmitt 2003). Treatments will be maintained for up to five years and the subsequent effects on coral growth rates determined using methods previously described.

2.4. Maintenance and Functional Consequences of Diversity

A variety of theories have been forwarded regarding the maintenance of diversity in benthic marine systems (Chesson 2000). Some are based on the fact that local populations are demographically open [e.g., lottery hypothesis (Sale 1977), recruitment limitation hypothesis (Doherty 1983, Doherty & Fowler 1994), storage effect model (Chesson & Warner 1981, Warner & Chesson 1985)] while others are not [e.g., intermediate disturbance hypothesis (Connell 1978), niche diversification (Gladfelter & Gladfelter 1978, Ormond et al. 1996)]. We initially will focus on the latter class of models given that disturbance is a unifying theme among LTER sites. The role of disturbance in the maintenance of diversity in marine systems was elucidated by pioneering work on coral reefs (e.g., Connell 1978) and the rocky intertidal zone (e.g., Lubchenco 1978, 1982, 1983, Lubchenco & Menge 1978, Sousa 1979). Physical and biological disturbances on coral reefs are followed by a complex process of recovery that depends on timing and severity of perturbations, as well as the presence of other stressors (Glynn 1996, Connell 1997, Hughes & Connell 1999, Nystrom et al. 2000, Nystrom & Folke 2001, Karlson & Cornell 2002, Adjeroud et al. 2002). Large disturbances can result in long-lasting effects on the local community that arise from structural changes, differential recruitment, delayed mortality from altered predator-prey relationships or outbreaks of disease (Knowlton et al. 1981, 1990). The capacity of a local reef system to cope with short- and/or long-term disturbances, including gradual climate change, depends on such aspects as genetic variability within populations, diversity within and among functional groups, and connectedness of habitats (Connell 1997, Hughes & Connell 1999). However, both the mechanisms and temporal patterns of recovery following disturbances are not well understood in coral reef systems.

Understanding maintenance of diversity on coral reefs requires knowledge of relationships between the foundational species (corals) and the other organisms that live on the reef. Species vary greatly in their dependence on live coral (e.g., Bell & Galzin 1984, Bouchon-Navarro et al. 1985, Munday et al. 1997, Ault & Johnson 1998, Jones & Syms 1998, Munday 2000, Holbrook et al. 2002a, 2002b), and there can be strong direct and indirect interactions among anthozoans and the various species they harbor (Meyer & Schultz 1985, Liberman et al. 1995, Stachowicz 2001, Schmitt & Holbrook 2003). Such complex interactions have a critical influence on patterns of local diversity. In addition to understanding the association between corals, fishes and invertebrates, it is necessary to know how biotic interactions affect diversity and how disturbance mediates these interactions.

In addition to our incomplete understanding of the processes that maintain local diversity in reef systems, there is even less known about the functional consequences of diversity in these systems. The relationship between species diversity and ecosystem properties such as stability, resistance and productivity have been debated by ecologists for decades (MacArthur 1955, May 1974, McCann 2000, Loreau et al. 2001, 2003, Symstad et al. 2003). Diversity could influence ecosystem properties via higher productivity as more species may more fully use available resources (Ehrlich & Ehrlich 1981). By contrast, as diversity increases, species may become functionally redundant and thus richness may not correlate with ecosystem function (Lawton & Brown 1993). If only some species have strong effects on ecosystem function, it becomes necessary to examine the functional importance of species as well as species richness (Lawton 1994, Duffy et al. 2001). Although there has been some theoretical treatment of these issues (McCann 2000, Loreau et al. 2003), the empirical explorations of diversity effects on ecosystem function have been largely confined to studies in terrestrial environments, and the focus has been on diversity effects of primary producers (Tilman et al. 1997, Levine & D'Antonio 1999, Emmerson & Raffaelli 2000, McCann 2000, Loreau et al. 2001, 2003). A number of these studies have revealed positive relationships between diversity and ecosystem function (e.g., productivity, nutrient retention, invasion resistance), although the generality of the results to date has been debated actively (Loreau et al. 2001). Only a handful of studies have explored functional effects of diversity in marine systems, and they have focused on consumer groups (Stachowicz et al. 1999, 2002, Duffy et al. 2001, 2003, Emmerson & Raffaelli 2000, Emmerson et al. 2001). To our knowledge, this issue has not yet been explored in coral reef ecosystems. The current state of knowledge does not permit assessment of whether diversity affects ecosystem processes similarly in wide array of systems ranging from terrestrial to marine, yet clearly this insight is of critical importance to a complete understanding of ecosystem function.

During the initial years of the LTER, we will address two themes: (1) understanding the functional relationships between diversities of foundational species (corals) and associated fishes, and (2) exploring mechanisms underlying the response to and recovery following disturbance.

I) What are the functional relationships between foundational coral species and reef fishes?

Rationale: Assemblages of reef fishes can vary greatly in composition, richness, and relative and total abundances at the local scale. The amount of this variation that can be explained by quality or quantity of habitat has ranged from comparatively high to relatively little (Chabanet et al. 1997, Ault & Johnson 1998; Adjeroud et al. 1998, Jones & Syms 1998; Syms & Jones 2001, Eagle et al. 2001, Holbrook et al. 2000, 2002a, 2002b, McClanahan & Arthur 2001). Commonly, strong associations have been found for species with narrow habitat requirements that were sampled at small spatial scales (Bell & Galzin 1984, Syms 1995, Munday et al. 1997, Holbrook et al. 2000, Munday 2000, Schmitt & Holbrook 1996, 2000). In addition, habitat complexity and/or species diversity of corals can be relatively good predictors of overall abundance or species richness of the fish assemblage (Gladfelter & Gladfelter 1978, Gladfelter et al. 1980, Bell et al. 1985, Roberts & Ormond 1987, Ormond et al. 1996, Friedlander & Parrish 1998, Jones & Syms 1998, Ohman & Rajasuriya 1998, Holbrook et al. 2002a. 2002b, Holbrook & Schmitt 2003). While these relationships tend to be positive, especially at low absolute levels of coral cover (Jones & Syms 1998), they have been infrequently explored across a wide range of coral cover within the same local reef environment. In fact, if diversity of coral is responsible for the positive relationships observed in earlier studies, the relationship between fish species richness and total cover of coral could be unimodal because for

coral, species richness and cover is a hump-shaped function (Connell 1978, Jones & Syms 1998). A similar hump-shaped pattern has been observed in the Western Pacific (G. Jones, pers. comm.), and we have preliminary evidence that this is the case on Moorea (Holbrook et al. unpub data). We propose surveys and experiments to test the relationship and explore underlying mechanisms.
Approach: We will use surveys and correlative studies to quantify the relationship between substrate diversity and species richness of fishes. Surveys will vary with respect to location (fore reef, lagoons), habitat type (continuous reef, patch reefs), and spatial scale (10 to 1000 m^2), to explore whether the relationship between species richness of fish and corals (and live coral cover) is similar across spatial scales and habitat types. In addition, we propose an experiment to test the relationship between coral and fish diversity and to estimate the effect of coral diversity on primary productivity. Experimental patch reefs (each 3 m^2) will be constructed on sandy bottom in the lagoon. These will have intermediate (50%) and high (100%) cover of corals, and will vary in species richness (from 1 to 6 species, N=6 replicates of each). Treatments will be reefs composed entirely of each species, reefs containing 2 of the species, 4 of the species and all 6 of the species. Three species of corals with an open, branching growth form (e.g., *Acropora* sp., *Pocillopora* sp.) and three species with a mounding growth form (e.g., *Porites* sp., *Montipora* sp.) will be used, with growth form represented equally in treatments containing more than one species. We have made patch reefs in the lagoons at Moorea and have found growth and survival of the corals to be excellent over several years. Following establishment, reefs will be surveyed ~ 3 times each year to assess temporal patterns of species richness, total abundance of fish and other invertebrates, trophic structure, species composition, and primary productivity.

II) What mechanisms underlie response to and recovery following disturbance?
Rationale: Recent studies of taxonomic and functional composition of reef fish assemblages have suggested that, on biogeographic spatial scales, there are predictable patterns of community structure (Bellwood & Hughes 2001, Bellwood et al. 2002). Further, there was substantial similarity in functional composition among similar reef habitats (that varied in wave exposure) between biogeographically separate areas (Pacific and Caribbean; Bellwood et al. 2002). These results suggest that at the largest spatial scales, assembly rules strongly influence taxonomic composition, such that the proportion of species at the Family level is highly predictable, and that assembly rules based on function may operate at local spatial scales. If true, this suggests that following disturbances, fish assemblages should "reassemble" in a predictable way. Although there has been much empirical work on the effects of disturbance on corals (e.g., Connell 1978, Connell et al. 1997, Harmelin-Vivien & Laboute 1986, Faure 1989, Fagerstrom 1992, Hughes & Connell 1999), and a number of studies of the responses of fish to natural disturbances that altered habitat (Bouchon-Navaro et al. 1985, Galzin 1987a, Sano 2000, 2001, Cheal et al. 2002, Adjeroud et al. 2002), almost no experimental studies have addressed disturbance and recovery for reef fishes (Jones & Syms 1998, Syms & Jones 2000, 2001). Early studies in which disturbances were applied by removing reef fishes and observing recolonization revealed unpredictability in community structure (Sale & Dybdahl 1975, 1978, Sale 1980). By contrast, more recent experiments involving removal of fishes from small patch reefs found that while assemblage structure "recovered" and was indistinguishable from control reefs within several months, removal reefs had significantly lower total abundances of fish that persisted throughout the two-year experimental period, despite the fact that there had been no disturbance to the reef substrates themselves (Syms & Jones 2000). Experiments to date have all been conducted on very small patch reefs, where demographic stochasticity could drive patterns of community recovery; assembly rules might prevail at larger spatial scales. Additional experiments that explore effects of disturbances and patterns of recovery of fish assemblages will be designed to gain insight into variation in resiliency of assemblages and the mechanisms that underlie recovery.
Approach: We will conduct perturbation experiments in which resident fish are removed from patches of habitat, and recovery of the assemblages is monitored for five years. These experiments will be done in two lagoon habitat types: continuous reef and patch reefs (5 m^2, 10m^2, 50m^2, & 100 m^2 in area) with a minimum of 4 replicates per treatment. Removal treatments will be: (i) all fish removed, (ii) only sedentary predators removed, and (iii) only planktivores removed. Coral and other substrates will be mapped, and fish will be counted prior to removals. Fish will be censused and mapped on all experimental and control plots ~ 3 times annually to determine patterns of species abundance and micro-habitat association. These experiments will enable us to assess the rate and

pattern of recovery following perturbation in a habitat-specific context, and to explore whether different portions of the fish assemblage recover more predictably than others.

3. Modeling and Synthesis

Each of the science themes in our proposed program will be supported by oceanographic and ecological modeling. Both are critical to the proposed research: the oceanographic models to characterize the physical forcing and population transport in the system, the ecological models to describe biological processes occurring on the reefs. Ecological modeling will involve detailed simulations of particular components of the system, as well as more general models that characterize the fundamental processes being studied. These latter models are the key to integrating the results of the individual empirical studies, to guiding the design of future empirical work, to relating the findings to other coral reef systems, and to comparison with other non-tropical systems (e.g., other LTER sites). Where possible, the simulations will be process based, and their design will be guided by insight from the process-based modeling.

Physical Circulation Models. Understanding the circulation of oceanic waters through the coral reefs and within the lagoons of Moorea is critical to understanding the overall role of flow in the function of the reef ecosystem. A variety of circulation models (e.g. Hearn 1996, Kraines et al. 1998) incorporating accurate bathymetry and coastline shape, driven by realistic forcing due to wind, wave breaking, tides, and buoyancy will be used to understand important flow parameters in the lagoons around Moorea. In particular, the dependence of residence times in the lagoons and flow speed at various locations over a wide range of forcing conditions will be explored. Transport and dispersion of nutrients and larvae into the lagoons will also be examined with modeling approaches. Models will be calibrated by using the extensive suite of current and water property observations obtained in support of the ecological studies. Additionally, dye studies and drifter releases will clarify pathways through the lagoons and refine trajectory predictions from the models.

Physiologically-based Models of Corals. Corals are functionally mixotrophs, deriving energy from both autotrophic and heterotrophic interactions. All studies of nutrient dynamics and energy flow in the reef will require a reliable baseline model of these interactions. Initial efforts will use the Dynamic Energy Budget (DEB) modeling approach, pioneered by Kooijman (1993, 2000). DEB models describe the acquisition of energy and elemental matter by organisms and its utilization for development, growth, reproduction, and maintenance in both static and variable environments. There is well-developed formalism for using DEB models as the core component of individual-based population and ecosystem models (Kooijman 2000, Nisbet et al. 2000). Our representation of corals will be based on a recent DEB model of mixotrophs (Kooijman et al. 2002) with mechanistic descriptions of both the autotrophic and heterotrophic processes. This model will allow quantitative investigation of changes in the environment that impact the fundamental mutualism. A population model for corals based on this representation will be used in food web studies (see below).

Population Dynamics in Open Systems with a Unidirectional Flow. Understanding population dynamics on a small island like Moorea involves confronting the so-called "drift paradox", according to which extinction is inevitable in a closed population subject only to unidirectional dispersal. There is a substantial body of literature to describe regional scale population dynamics and persistence in coastal systems with long-shore currents (Gaines & Bertness 1992, Alexander & Roughgarden 1996, Gaylord & Gaines 2000), but there is rather little theory that applies to systems comparable in size to the range of larval disperal within a single generation. Notable exceptions are Lewis et al. (1996), Ballyk et al. (1998), Ballyk & Smith (1999) and Speirs & Gurney (2001), none of which cover organisms with dispersal restricted to a single (larval) stage. A reinterpretation of some recent work on stream systems (Pachepsky et al. submitted), points to the importance for population dynamics of quantifying local retention of larvae. Thus for a few focal species (e.g., branching corals, planktivorous fishes), initial modeling will focus on obtaining a better understanding of the factors determining population persistence in the prevailing physical environment, and on modeling the processes that determine the spatial and temporal scales of response to environmental heterogeneity.

Food Web Modeling. Many of the individual food web interactions in coral reefs are well understood, but many indirect effects remain elusive. Detailed food web simulations will be constructed as required for understanding top-down, bottom-up, and other disturbances, but early in the research we intend to develop a suite of simplified, process-based models capable of describing the potential stable states for the system (e.g. domination by algae versus corals). The representation of corals will be based on the DEB model described above, allowing modeling of nutrient inputs and recycling as well as population changes (e.g. removal of top predators) within a single model. The initial phenomena to be explored will mirror the research projects delineated in section 2.3 above.

RELATIONSHIP OF PROPOSED WORK TO INTER-LTER SITE RESEARCH ACTIVITIES

The proposed Tahitian Coral Reef LTER will make strong contributions to a number of major themes that are becoming important throughout the LTER network. These include, among others, effects of human and climatic disturbances on ecosystem function and structure (at the landscape scale), the maintenance and functional roles of biodiversity, and effects of spatial heterogeneity in physiochemical conditions on ecosystem processes. A coral reef LTER at Moorea would make a unique contribution to Network activities in these and other areas. The coral reef ecosystem is not represented in the LTER Network, yet is one of the most ecologically important – and potentially threatened – ecosystems in the marine environment. There are natural bridges that can be built with existing LTER sites that would facilitate highly informative cross-site comparisons. For example, our theme of dynamics of a physically forced system is one that is common to several LTERs. The Santa Barbara Coastal LTER, for instance, is exploring long-term dynamics of giant kelp forests in the physically forced temperate marine environment. Similar to corals, giant kelp is the major biogenic structuring feature and is the foundational species in that ecosystem; giant kelp and corals no doubt have very different dynamics owing to differences in life history attributes and their responses to similar changes in abiotic and biotic conditions. We also envisage rich comparisons with sites that involve life in a moving fluid (Palmer Antarctic LTER, North Temperate Lakes LTER), as well as with terrestrial sites regarding general ecological issues (e.g., functional consequences of diversity) and processes (e.g., abiotic forcing).

RESEARCH / SITE MANAGEMENT PLAN

The management plan for the Tahitian Coral Reef LTER encompasses (i) program governance, (ii) resource allocation and acquisition among projects and components, (iii) relations with agency, University, government partners, and the public, (iv) interactions with the LTER network and individual LTER sites, and (v) day-to-day operations. As lead investigator, Russell J. Schmitt will serve as the primary point of contact with NSF, the LTER Network, campus administrative units, the administrative entities of the UC Richard Gump Research Station and the appropriate agencies of the Territorial Government of French Polynesia. He will be responsible for the day-to-day operations of the program and for overseeing the implementation of all program components. He will be assisted by a half-time Deputy Program Director (Andrew Brooks), who also will supervise the Data Management component and the Tahitian Coral Reef LTER web site. A half-time Education and Outreach Coordinator (Allison Whitmer) will be responsible for all of the program's outreach and educational activities, including those in French Polynesia involving coordination with Atitia Education Center staff. Strategic planning of major tasks, research direction, policies, initiatives and project resource allocation and acquisition will be decided on by consensus of a nine-person Executive Committee, which will meet semi-monthly (alternating between UCSB and CSU Northridge). In addition to the four Co-PIs (R. Schmitt, R. Carpenter, P. Edmunds, S. Holbrook), five other members of the Executive Committee will be chosen to represent broadly the participating disciplines. Minutes of Executive Committee meetings will be made available to all Associate Investigators. The Program and Deputy Program Directors and the Executive Committee will be assisted by a part-time administrative assistant.

Day-to-day running of the LTER will be done by several professional staff members. The Deputy Program Director, assisted by a Staff Research Associate, will act as coordinator of all field work activities; we anticipate that the Staff Research Associate will spend the majority of his/her time in Moorea. A computer network technologist will serve as the LTER's database manager and will work closely with the Executive Committee in developing database design and management; s/he will be the point contact for interactions with database managers at the other LTER sites.

We will hold all-day retreats annually for all participants in the LTER to insure coordination within the program and to enhance interdisciplinary discussions. All PIs, Associate Investigators, staff and students will attend the annual meetings. We also will meet regularly to plan upcoming research and address issues related to synthesis and integration of the research components and disparate types of data being collected.

Table 1. List of participating investigators in the Tahitian Coral Reef LTER.

Individual	**Affiliation**	**Area of Expertise**
Russell J. Schmitt (Lead PI)	UCSB	*Population dynamics of fishes & invertebrates*
Robert Carpenter (Co-PI)	CSUN	*Coral reef trophodynamics / productivity*
Peter Edmunds (Co-PI)	CSUN	*Physiological ecology of stony corals*
Sally Holbrook (Co-PI)	UCSB	*Community ecology of fishes*
Alice Alldredge	UCSB	*Zooplankton ecology*
Giacomo Bernardi	UCSC	*Population genetics of fishes*
Andrew Brooks	UCSB	*Community ecology of fishes*
Craig Carlson	UCSB	*Marine microbial ecology /organic cycling*
Joseph Connell	UCSB	*Community ecology*
Ruth Gates	Univ. Hawaii	*Population genetics of coral & symbionts*
Gretchen Hofmann	UCSB	*Ecological physiology of marine animals*
David Lea	UCSB	*Paleoceanography & paleoclimatology*
James Leichter	UCSD / SIO	*Physical – biological coupling*
Hunter Lenihan	UCSB	*Marine stressor – demography linkages*
Sally MacIntyre	UCSB	*Hydrodynamics & ecosystem ecology*
Stephane Maritorena	UCSB	*Remote sensing of coral reefs & ocean waters*
Roger Nisbet	UCSB	*Ecological modeling*
Libe Washburn	UCSB	*Physical oceanography & modeling*
Allison Whitmer	UCSB	*Physiological ecology of algae*
Susan Williams	UCD / BML	*Nutrient dynamics in reef environments*

Table 2. Proposed monitoring strategy.

Monitored Variable	*Locations Monitored*	*Primary Monitoring Method*	*Frequency of Monitoring*
Abiotic:			
Large Scale -			
Climate (weather) data	French Polynesia	Satellites & Met. Stations (Meteo France)	Daily
Tides	French Polynesia	Remote sensing (TOPEX-Poseidon, ERS) and tidal analysis Pressure sensors around Moorea	daily predictions half hourly
Regional surface currents	French Polynesia	Remote sensing (TOPEX-Poseidon, ERS)	few days to weekly
Sea-surface temperature	French Polynesia	Remote sensing (AVHRR)	daily (when clear)
Subsurface [Chl a]	French Polynesia	Remote sensing (SeaWiFS, MODIS)	daily (when clear)
Light absorption/particulate backscattering	French Polynesia	Remote sensing (SeaWiFS, MODIS)	daily (when clear)
Small Scale -			
Climate (weather) data	Cook's Bay	Gump weather station	15 minutes
pH	Moorea – 1 site/side	Standard pH meter	1^o Sites: Weekly 2^o Sites: Periodically
Sedimentation	Moorea – 1 site/side	Standard sediment columns	Monthly
Waves (offshore pressure)	Moorea – 1 site/side	Seabird (SBE-26) pressure sensors	5 minutes/hour over 6 months
Flow (lagoonal and island wide)	Moorea – 1 site/side	Acoustic Doppler current profilers	Every 5 minutes over 6 month period
Water temperature	Moorea – all sites	1^o Sites: Seabird (SBE-39) thermosalinographs 2^o Sites: Onset tidbits	1^o Sites: Every minute per 6 months 2^o Sites: Every 5 minutes
UV and surface irradiance	Moorea – 1 site/side	Recording surface light meters	Every 5 minutes during daylight
Salinity	Moorea – 1^o sites	Seabird (SBE-39) thermosalinographs	Every minute over 6 month period
Turbidity	Moorea – 1^o sites	Seabird (SBE-39) thermosalinographs	Every minute over 6 month period
PAR	Moorea – 1^o sites	Seabird (SBE-39) thermosalinographs	Every minute over 6 month period
Dissolved nutrients	Moorea – 1^o sites	Field collection and laboratory analysis	1^o Sites: Weekly 2^o Sites: Periodically
POC	Moorea – 1^o sites	Field collection and laboratory analysis	1^o Sites: Weekly 2^o Sites: Periodically
PON	Moorea – 1^o sites	Field collection and laboratory analysis	1^o Sites: Weekly 2^o Sites: Periodically
Water column optical properties	Moorea – 1^o sites	Satlantic ac9 - in water radiometry	Variable

Table 2 - continued.

Monitored Variable	*Locations Monitored*	*Primary Monitoring Method*	*Frequency of Monitoring*
Biotic:			
Individual Level -			
Physiology (key species[1])	Moorea – all sites	PAM fluorometry, G.S.I.	Variable
Growth	Moorea – all sites	Buoyant weighing, length/weight measures	Variable
Population Level -			
Abundance (key groups[2])	Moorea – all sites	Transects	Variable
Age/Size structure (key species[1])	Moorea – all sites	Transects	Variable
Settlement/Recruitment (key species[1])	Moorea – all sites	Settlement plates, recruit transects	Variable
Coral cores	Moorea – all sites	Cores	Once every 5 years
Community Level -			
Diversity (key groups[2])	Moorea – all sites	Transects	Variable
Ecosystem Level -			
Primary productivity -			
Reef	Moorea – all sites	Upstream-downstream respirometry Lab measurements of key groups	Semi-annually
Water column	Moorea – all sites	^{14}C tracer/bottle techniques	Multiple times per week
Reef cover		Remote imaging (Satellite/aerial photos)	Once per three years

[1] Key species include: Algae- *Hydrolithon* spp., *Polysiphonia sparsa, Turbinaria ornata*; Corals- *Acropora* spp., *Montipora sp*., *Pocillopora eydouxi, Pocillopora meandrina, Pocillopora verrucosa, Porites rus, Porites lobata*; Other Invertebrates- *Acanthaster planci, Culcita nouvaguineae, Diadema savignyi, Diadema setosum, Echinometra matheai, Echinothrix calamaris, Heteractis magnifica, Tridacna maxima*; Fishes-*Amphiprion chrysopterus, Chaetodon citrinellus, Chaetodon lunulatus, Chaetodon vagabundus, Chromis viridis, Dascyllus aruanus, Dascyllus flavicaudus, Dascyllus trimaculatus*, *Paracirrhites arcatus Pomacentrus pavo, Scarus sordidus, Scarus psittacus*

[2] Key groups include: Algae-Corallines, Turf; Corals- Acroporids, Pocilloporids, Poritids; Other Invertebrates- Reef associated, demersal and benthic zooplankton, Asteroids, Crabs, Echinoids, Mollusks; Fishes- Acanthurids, Apogonids, Chaetodontids, Cirrhitids, Holocentrids, Labrids, Pomacentrids, Scarids, Serranids

Table 3. Examples of the abundance and major taxa of zooplankton in French Polynesia. Lagoon net zooplankton are considerably more abundant at night and occur in higher abundances than holoplankton in the surrounding ocean. Demersal plankton is shown as number of animals emerging per m^2 per night from benthic (mostly sand) habitats.

Plankton	Location	Time	Abundance	Major taxa	Source
Demersal Plankton only	Moorea Lagoon	Night	898-1222 m^{-2} $night^{-1}$	Harpaticoids, Ostracods, Crab larvae, Amphipods	Alldredge Unpub. data
	Moorea Lagoon	Night	1900- 10,650 m^{-2} $night^{-1}$	Copepods, Crab larvae	Renon & Lefevre 1985 Renon et al. 1985
Total Plankton	Tahiti Lagoon	Night	60 mg m^{-3}	Copepods, Ostracods, Larvae, Amphipods, Polychaetes	Renon 1978
	Tahiti Lagoon	Day	10 mg m^{-3}	Copepods, Appendicularians, Lucifer	Renon 1978
	Takapoto Lagoon (Tuamotu)	Night	1,595, 000 m^{-3} 54-170 mg m^{-3}	Copepods, Appendicularians, Decapod larvae, Chaetognaths, Amphipods	Renon 1977
	Takapoto Lagoon (Tuamotu)	Day	96000 m^{-3}	Copepods, Appendicularians, veligers	Renon 1977
	Takapoto Oceanic (Tuamotu)	Night	12 mg m^{-3}	Copepods, Appendicularians, Chaetognaths	Renon 1977
	Moruroa Lagoon (Tuamotu)	Night	425-783 mg m^{-3}	Copepods, appendicularians, Ostracods, decapod Larvae	Michel 1969
	Moruroa Oceanic (Tuamotu)	Night	24 mg m^{-3}	Copepods, Chaetognaths Appendicularians	Michel 1969

Figure 1. The location of French Polynesia in the central South Pacific **(top)**, the various island groups of French Polynesia **(middle)**, and the location of Moorea in the Society Islands **(bottom)**.

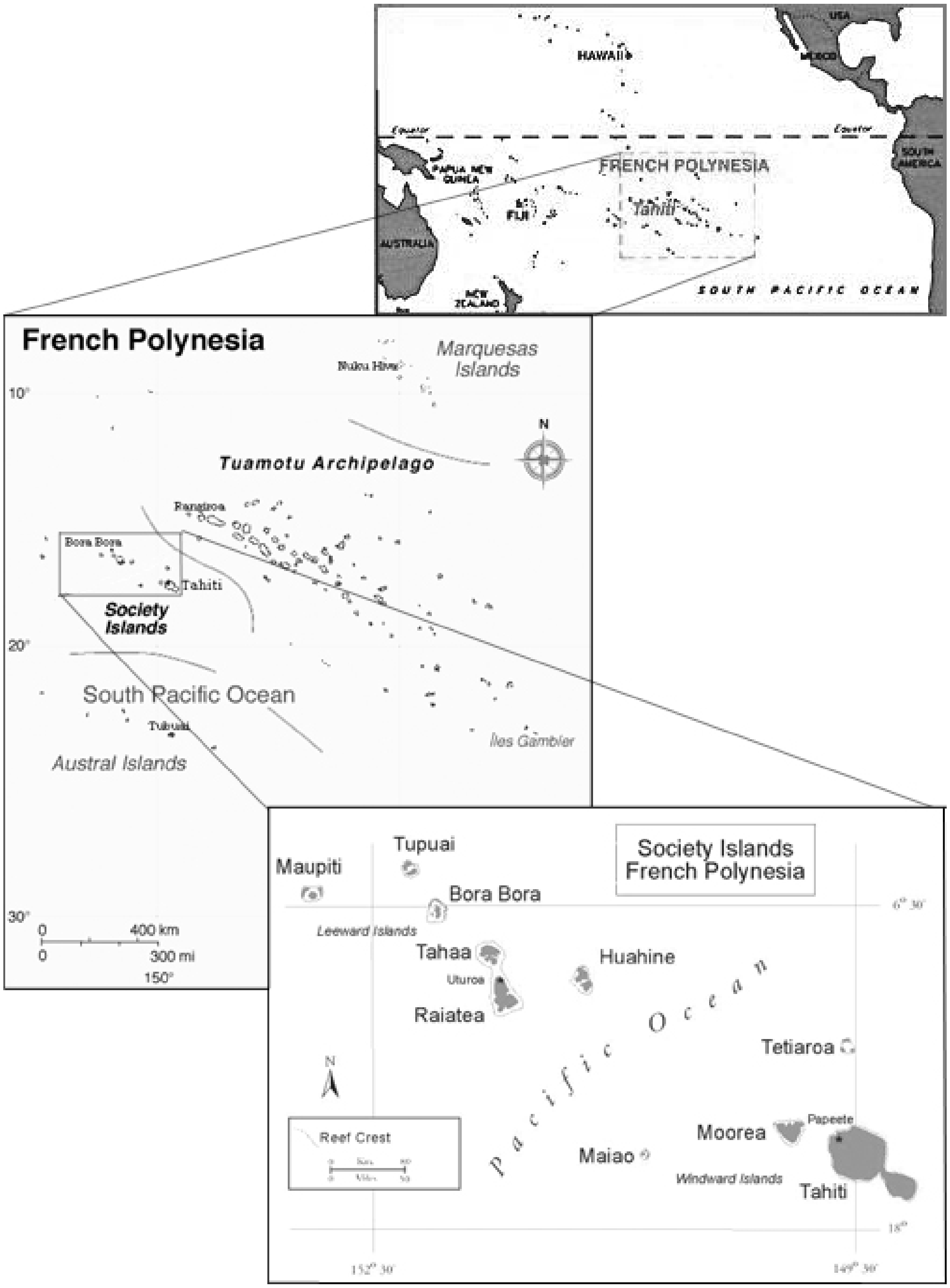
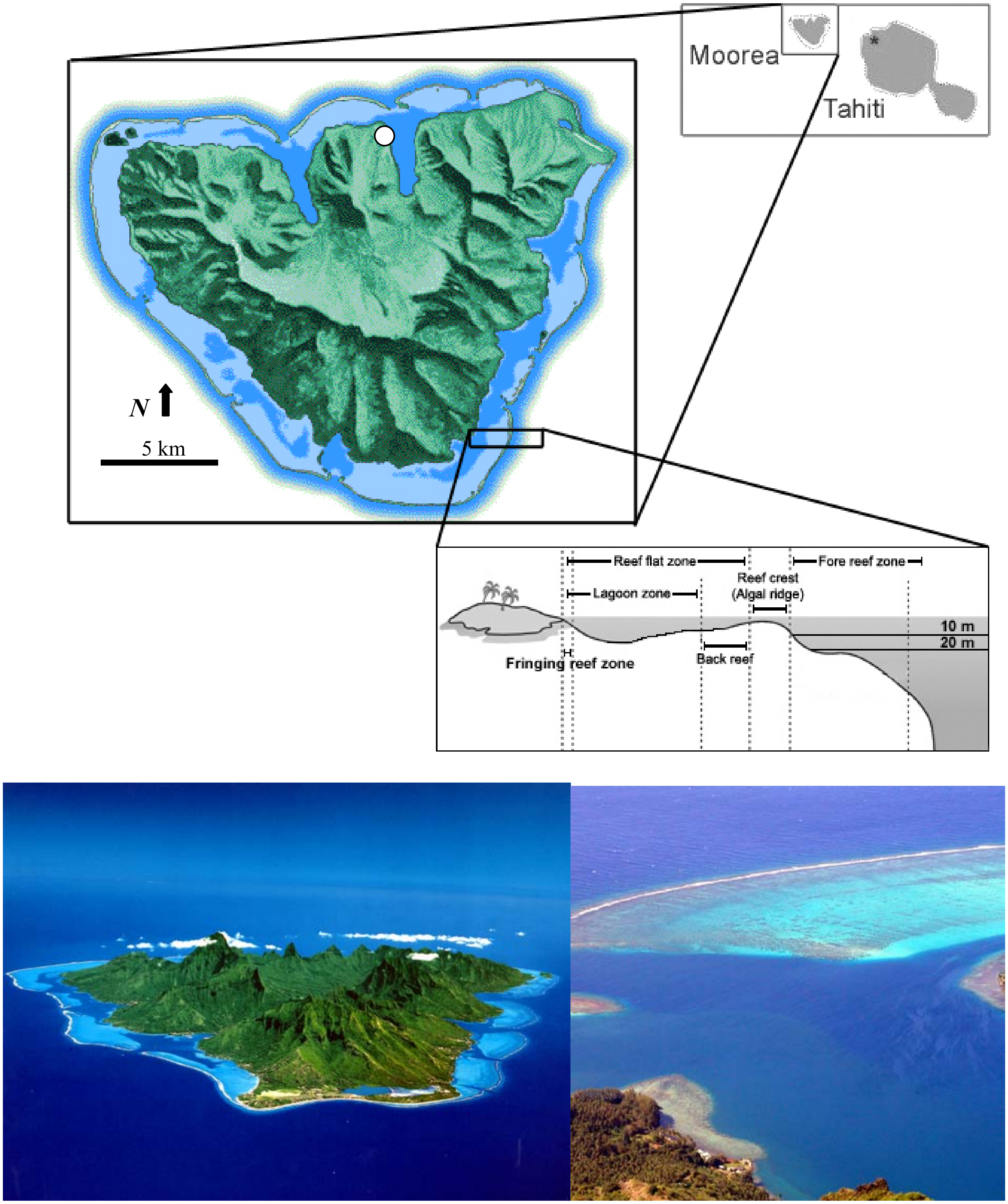


Figure 2. **(top)** Island of Moorea, 20 km east of Tahiti, showing the system of lagoons formed by a barrier reef that encircles the 60 km perimeter shoreline (white circle indicates location of the UC Gump Research Station); the insert illustrates a typical cross-section from shore to the steeply sloping fore reef. **(bottom left)** Photograph of Moorea with the northeast corner in the foreground. **(bottom right)** Photograph of the Gump Research Station property (at lower left of photograph) looking northeast to the Maharepa Lagoon back reef and reef crest.



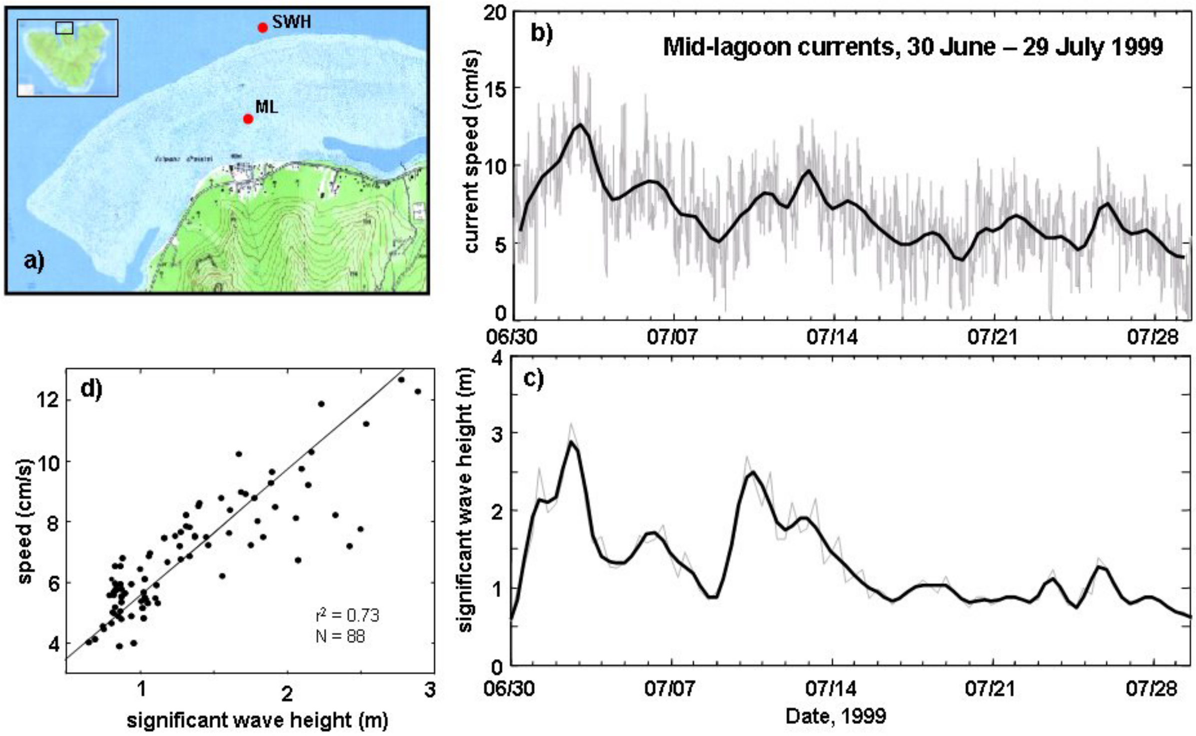


Figure 3. Time series from summer 1999 show dependence of current speed on significant wave height (SWH) at a reef on the north shore of Moorea. **(a)** Inset and small rectangle show study area on Moorea. Larger map of study area shows locations of bottom pressure sensor for estimating SWH (red circle labeled SWH) and mid-lagoon current meter (red circle labeled ML). **(b)** Time series of current speed at ML every 10 min (gray line) and smoothed with 36-hour low pass filter to remove tides (black line). **(c)** Time series of SWH measured every eight hours (gray line) and smoothed with 36-hour low pass filter (black line). **(d)** Scatter plot shows clear relationship between SWH and current speed at ML. Correlation between SWH and current speed is significant with r^2 = 0.7 3. Other processes such as variable wave direction and wind forcing may account for the scatter between current speed and SWH. (Washburn, Holbrook & Schmitt unpub. data)

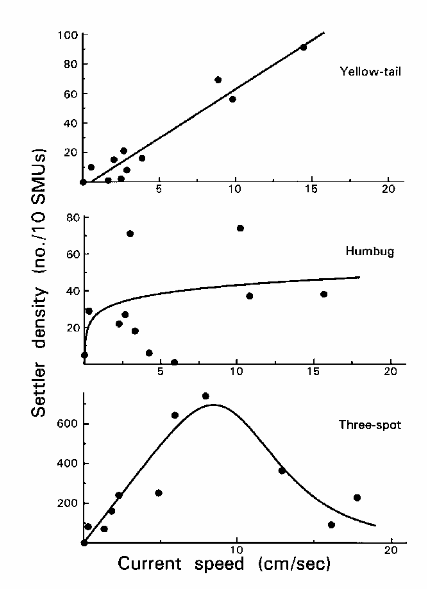


Figure 4. Relationships between variation in current speed and concurrent settlement of three species of damselfishes in lagoons at Moorea. Data are the number of larval settlers to 10 standard microhabitat units (SMUs) per week at the same 11 sites around Moorea as a function of average current speed (V) during the period. A Shepherd (1982) model [$S = \alpha V / (1 + \beta V^m)$] fitted to the data revealed that **(top)** a linear model was the best fit for yellow-tail dascyllus (*Dascyllus flavicaudus*) (r^2 = 0.93), **(middle)** a saturating model for humbug dascyllus (*D. aruanus*) (r^2 = 0.24), and **(bottom)** a hump-shaped model for three-spot dascyllus (*D. trimaculatus*) (r^2 = 0.89). (Schmitt & Holbrook 2002a, 2002b)

Figure 5. Temporal trends in abundance of the damselfish *Dascyllus trimaculatus* on 3 reefs at Moorea since 1992. Juvenile *D. trimaculatus* shelter in sea anemones (*Heteractis magnifica*) but adults are free-living. Abundance of adults **(a)** but not juveniles **(b)** doubled over time, mirroring the doubling in anemone cover **(c)** since 1992. Variation in juvenile abundance reflected more of the annual variation in daily settlement rates **(d)** of *D. trimaculatus* (estimated from daily counts of settlers to empty anemones on Gump reef from June – August annually). These data indicate that adult dynamics largely are driven by the dynamics of the juvenile resource and suggest that density-dependence influences juvenile throughput to the adult stage. (Schmitt & Holbrook unpub. data)

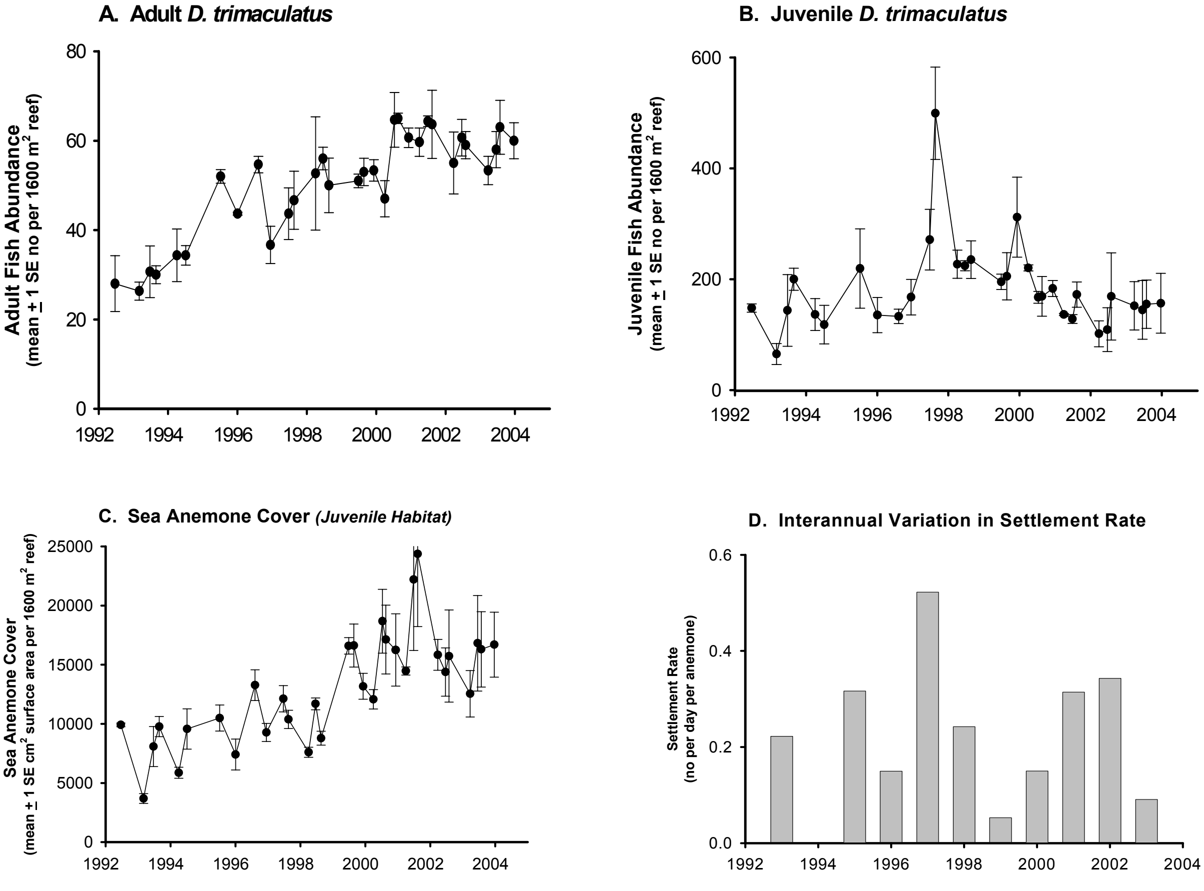


Figure 6. "Proof of concept" for one of our proposed approaches to forecast ecological performance of corals at Moorea using physiological-based analyses. Three species of pocilloporid corals were studied at One Tree Island (OTI) with the goal of integrating physiological analyses of coral growth with a size-based demographic model to develop the capacity to project population structure under defined environment conditions (Edmunds in prep. for *Ecological Applications*). This goal was achieved through: (1) a field analysis of population dynamics to establish Leslie Matrices for a single year, (2) laboratory analyses of growth rates to determine the effect of temperature, and (3) the development of a model that allowed population structure to be projected and analyzed for sensitivity to changes in critical parameters (e.g., birth rates, etc.). For the pocilloporids at OTI, the results show that the three species were not at equilibrium when initially sampled, and that the dynamics of only one of them (*S. hystrix*) was influenced substantially by increases in temperature as high as 4°C above present day levels. (Edmunds unpub. data)

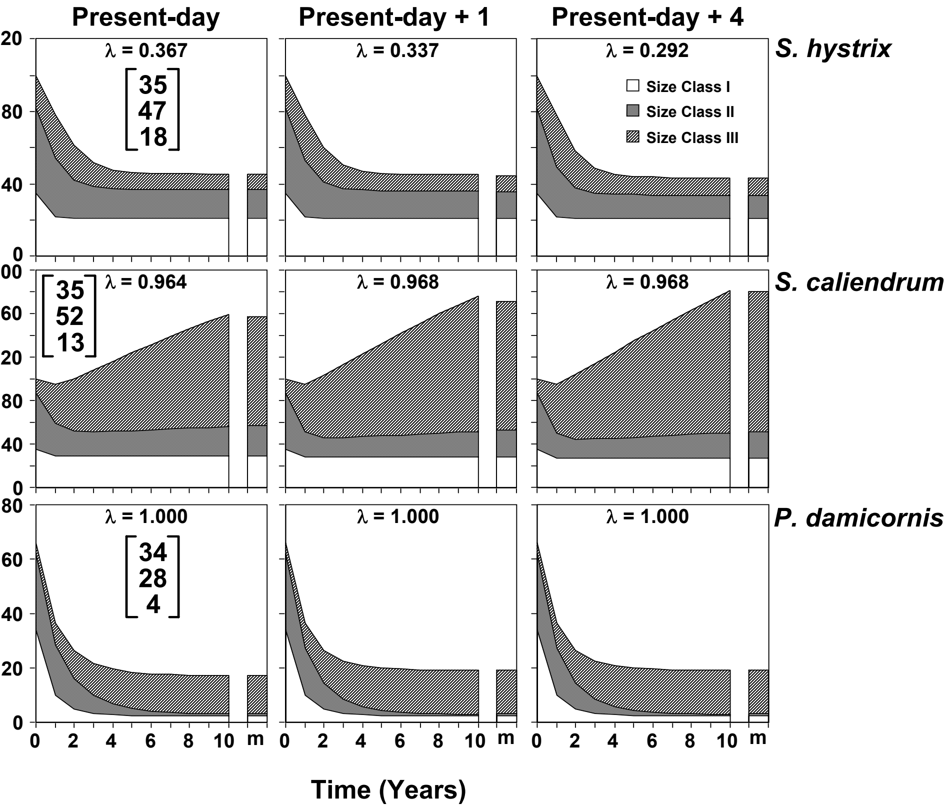


Figure 7. Relationships between size (volume) of a patch reef and **(top)** the mean log total abundance of resident fishes and **(bottom)** mean species richness of resident fishes. Two types of patch reefs are shown: reefs formed by *Porites rus* (n=39) and reefs formed by *Porites lobata* (n=57). (Holbrook et al. 2002b)

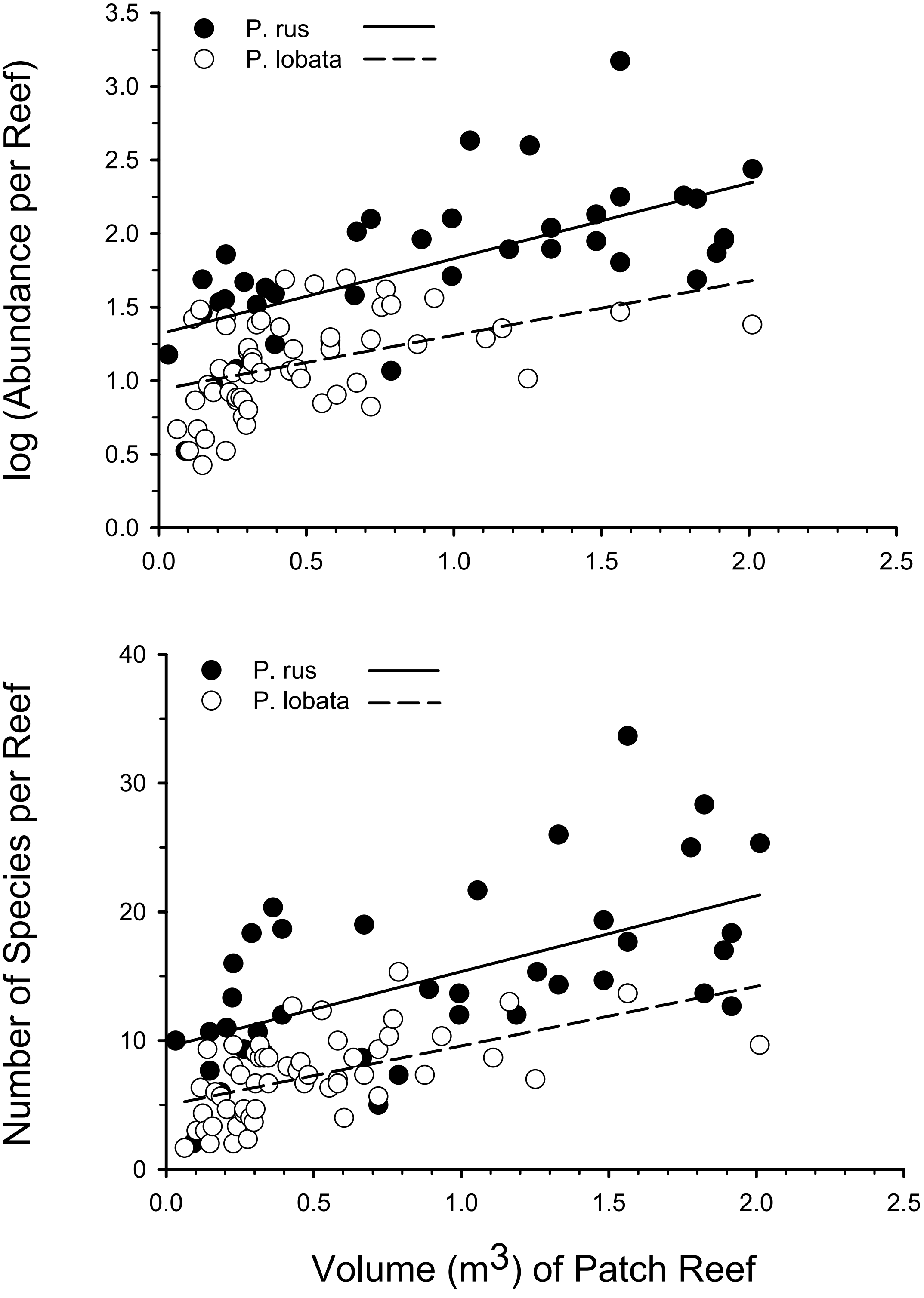


Figure 8. Larvae from the Caribbean coral *Porites astreoides* were tested for the effects of short term exposure to a range of seawater temperatures to better understand how temperature can mediate larval development, longevity and settlement patterns (Edmunds, Gates, Hoegh-Guldberg and Leggatt, in prep.). The treatments were provided by an aluminum block that created a thermal gradient in which larvae were incubated in glass test tubes for 24h. The results demonstrate the sensitivity of coral larvae to seawater conditions, and therefore the potential effects of abiotic conditions in driving patterns of coral recruitment. Specifically, the results for the zooxanthella content **(top)** and size of *Porites* larvae **(bottom)** show that they are sensitive to thermal effects lasting only 24 h and have a strong thermal maximum that is similar to ambient seawater temperature (i.e., their physiology is matched closely to seawater conditions). (Edmunds et al. unpub. data)

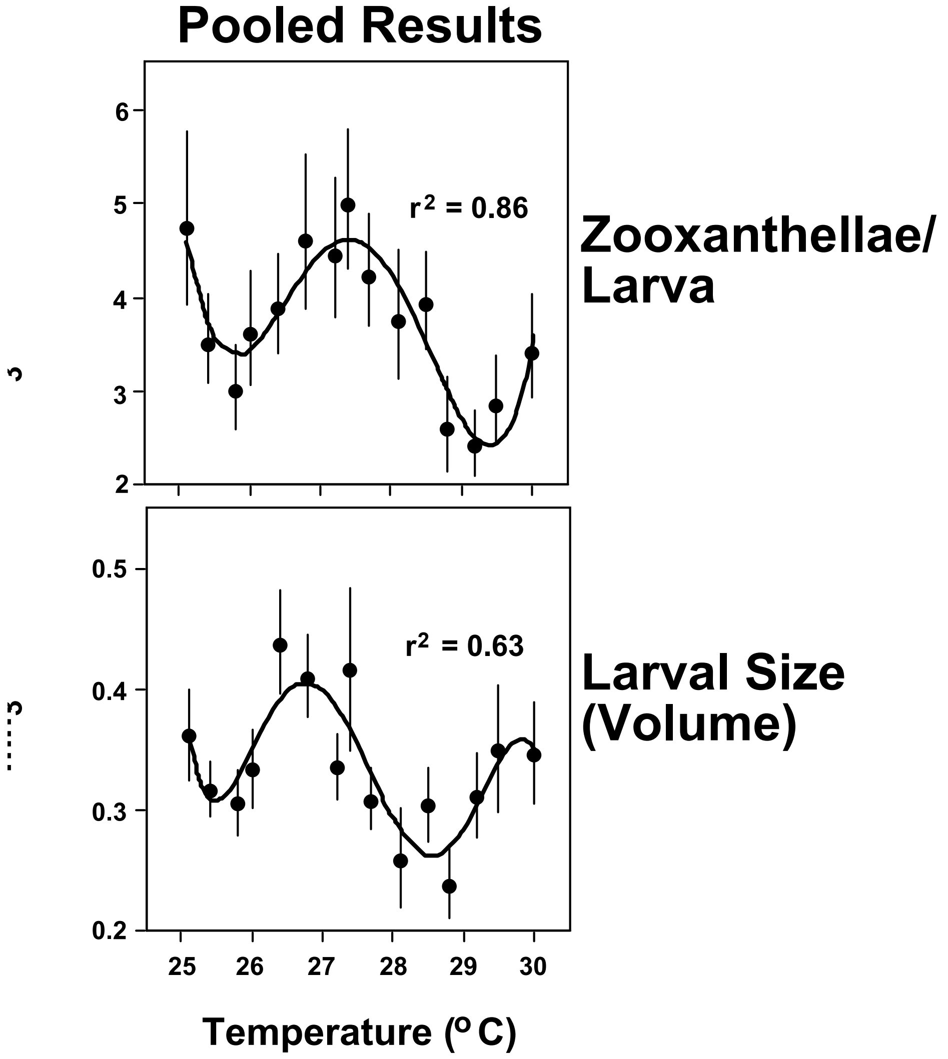


Figure 9. Performance over four months of coral fragments outplanted on artificial reefs having either high (0.75 m) or low (0 m) relief; fragments also were outplanted on 0.75 m high poles to control for confounding effects of height above the bottom and flow. Species outplanted included a species of *Acropora* (probably *A. elseyi*), *Pocillopora eydouxi*, and *Porites rus*. Shown are **(a)** mean (±1 SE) flow speed in each treatment, **(b)** effects of relief (flow) on coral growth plotted as mean changes (±1 SE) in fragment height, **(c)** effects of relief (flow) on coral survivorship plotted as the mean percentage (±1 SE) of each fragment alive after four months, **(d)** effects of relief on rates of corallivory plotted as the mean number of bite marks (±1 SE) observed per fragment of *Pocillopora* over four months and **(e)** the mean abundance (±1 SE) of corallivorus butterflyfishes, predominantly *Chaetodon citrinellus* and *Chaetodon vagabundus*, observed within blocks of each treatment type. In two of the three coral species, growth was greater but survivorship was lower on high relief (higher flow) relative to low relief reefs. There was more predation by butterflyfishes on high relief blocks and more butterflyfishes were associated with high relief reefs. (Brooks and Lenihan, unpub. data)

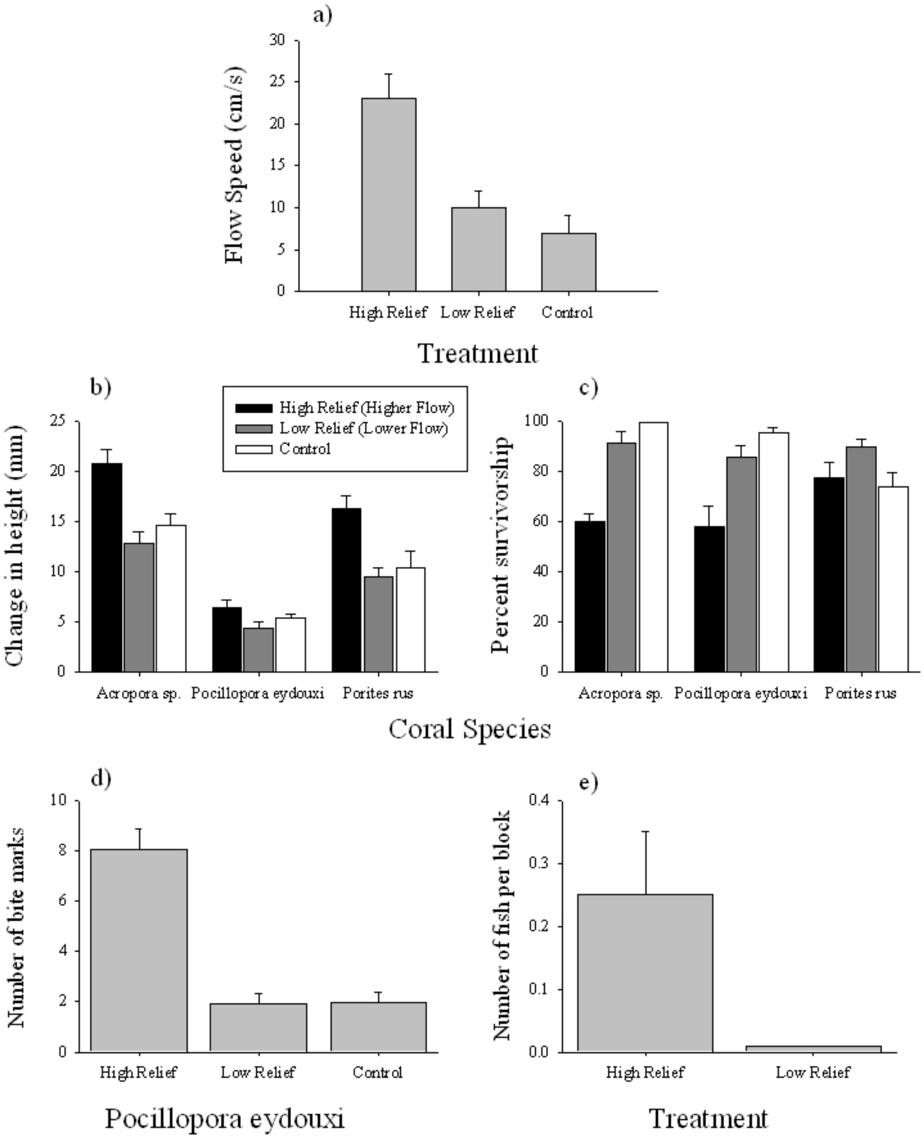


Figure 10. The effect of flow on the growth of transplanted coral fragments of **(a)** *Pocillopora eydouxi* and **(b)** *Acropora* sp. (probably *A. elseyi*) plotted as the mean (± 1 SE) change in height over four months. Coral fragments were transplanted to experimental reefs of differing height (0.1, 0.5, and 1.5m) which generated different rates of flow (5-8, 11-15, and 21-27 cm/s respectively) in lagoons along the north shore of Moorea, French Polynesia. Cages were employed to exclude corallivorous fishes (largely Chaetodontids and Scarids). Growth in *Pocillopora eydouxi* was greatest at intermediate flow speeds and was slightly greater in the absence of corallivores. For *Acropora sp.*, growth rates increased with increasing flow speed and with protection from corallivory. (Lenihan unpub. data)

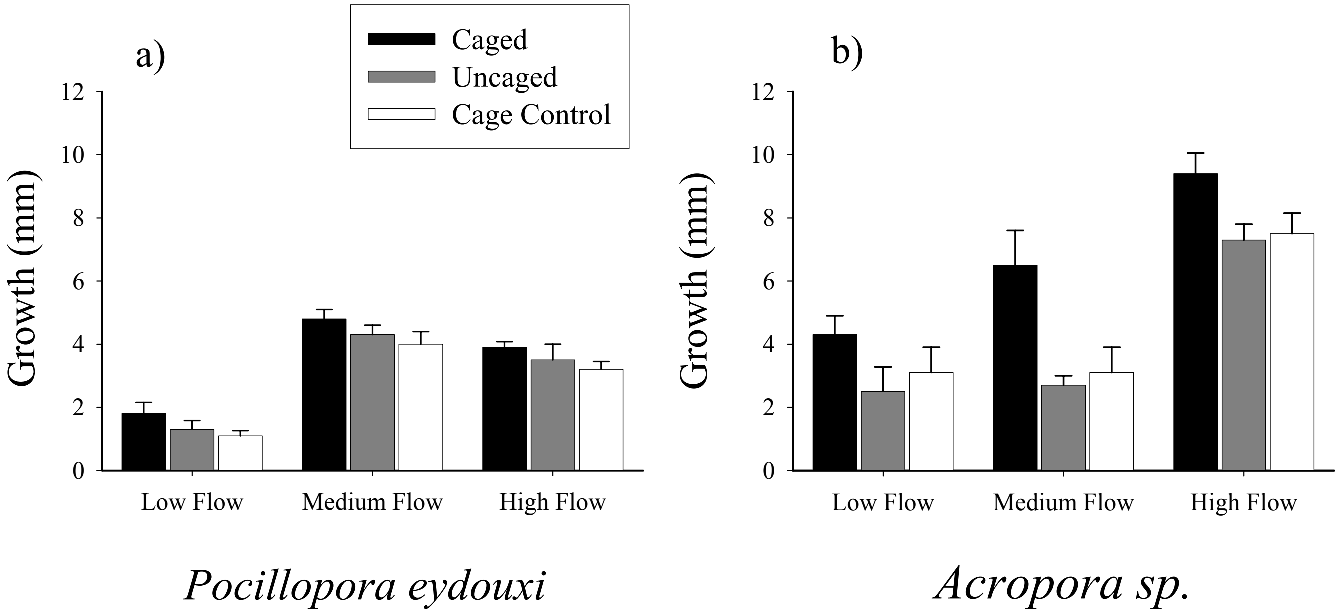


Figure 11. Net community primary production of the Kane'ohe Bay, HI barrier reef flat as a function of flow during the summers of 1999 and 2000. Open symbols are for high/constant light days, closed symbols are for low/fluctuating light days. (Carpenter unpub. data)

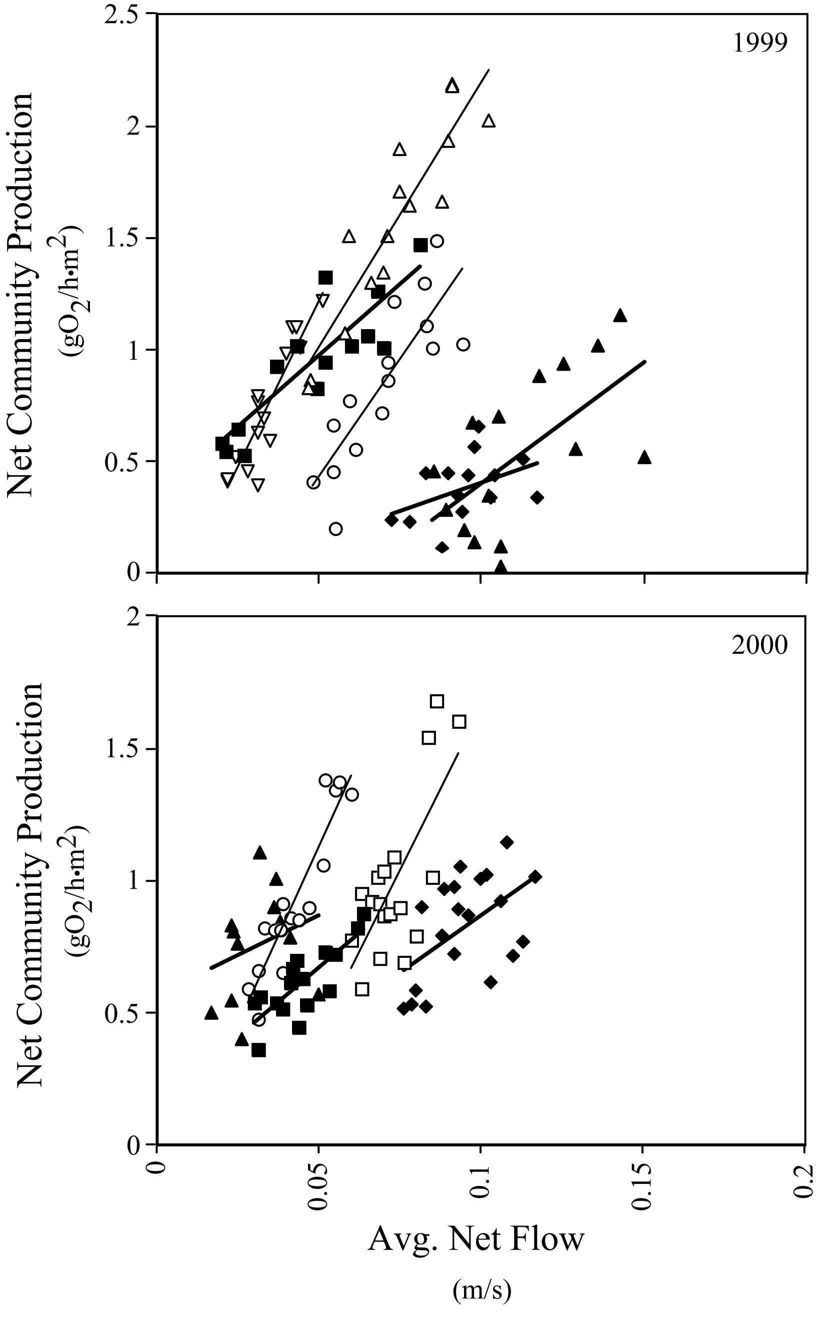
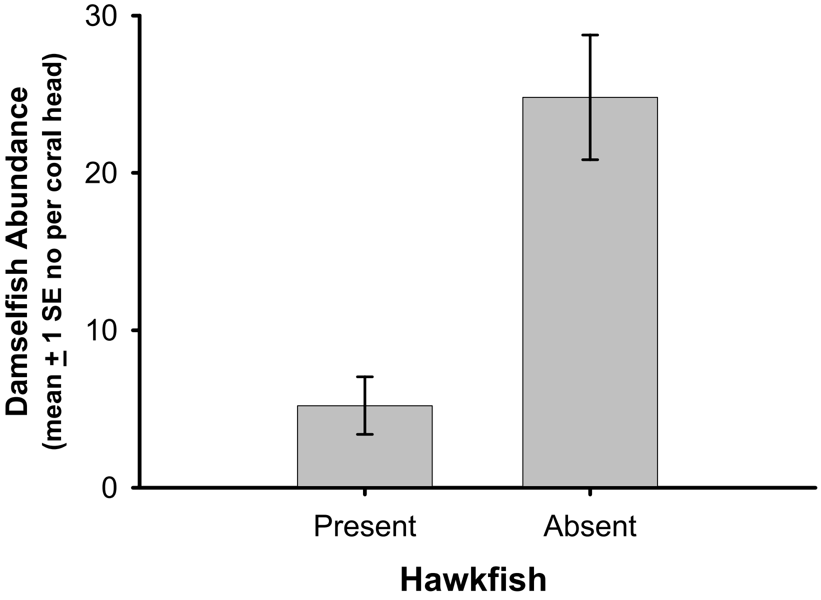
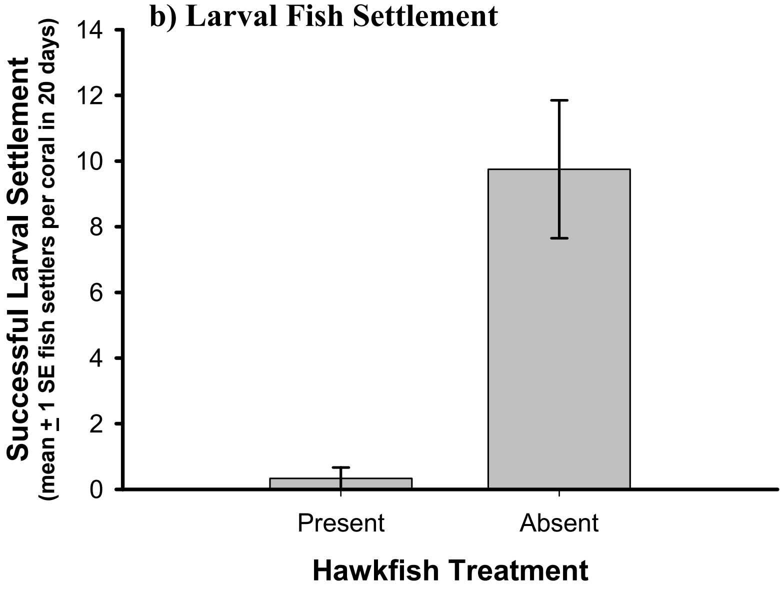


Figure 12. Effect of the presence of arc-eye hawkfish (*Paracirrhites arcatus*) on **(a)** abundance of damselfish on branching coral *Pocillopora eydouxi* and **(b)** successful settlement of larval fishes to *P. eydouxi* at Moorea. Data for (a) came from surveys 3 years after 60 outplanted heads of *P. eydouxi* were naturally colonized by fishes; 14 heads were colonized by hawkfish. For (b), hawkfish presence was manipulated by transplanting the predator to half of 20 *P. eydouxi* heads (randomly chosen) that were outplanted in a linear array 5 m apart; corals were otherwise maintained empty and new fish settlers were counted and removed daily for 20 days. (Holbrook & Schmitt unpub. data)



a) Damselfish Abundance



b) Larval Fish Settlement

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DATA AND INFORMATION MANAGEMENT SYSTEM

Objectives of the Information Management Group

The primary objective of the Tahitian Coral Reef (TCR) LTER Information Management (IM) group will be to facilitate current and future research and outreach efforts by providing readily accessible and robust software and hardware services. The IM group will consist of a Data Manager, a part time system administrator, a part time database specialist, and the Deputy Program Director, who will oversee IM activities and ensure strong linkages between research efforts and data management. The focus of the group will be on data organization and integrity, ease of access, and long-term preservation of the data archive and accompanying documentation. The group also will support communication among the participants in the LTER, its partners, outside agencies, and the public. Of particular importance is communication among the campuses involved, and with the actual site on Moorea; a dedicated DSL line at the Gump Research Station will be obtained to facilitate communication.

Data Sharing and Public Availability Policy

Data collected by the proposed LTER will be made available to the public without restriction. Our policy will be to make field data available on the web after we verify their quality and within a year of acquisition. Exceptions to this general rule fall into three categories: proprietary third-party information, ‘blackout’ periods for graduate student research, and results of process-oriented (experimental) studies. Proprietary information will be stored in the system only if its security can be reasonably guaranteed, and then only if critical to LTER research efforts. ‘Blackout’ periods will be allowed for graduate students until they complete their dissertations; nonetheless, the restricted data must be internally accessible, under the same data quality and consistency constraints as unrestricted information. In the case of process-oriented studies, data will be made available after papers have been accepted for publication or 3 years after completion of the process-oriented study, whichever comes first. The Executive Committee will be responsible for implementing all data management policies, including the schedule for researchers contributing their data to the LTER databases.

Facilities and Operation

The IM group will implement systems in an open, cross-platform environment that is based largely on Internet standards rather than vendor-specific technologies. This approach will leverage existing systems where possible and add new systems where necessary with a focus on collaboration and inter-operability, which reduces implementation costs and fosters communication. The TCR-LTER will leverage the UC Santa Barbara campus network and expertise from the Institute for Computational Earth Systems Science (ICESS). ICESS will provide the server-side software and hardware systems to support the TCR-LTER.

The UCSB research network infrastructure consists of a 1 Gigabit switched Ethernet backbone that connects departments and research units on campus. The ICESS computational facility is a shared, community resource designed to foster interdisciplinary and collaborative research and training. This facility currently includes the following: 55 UNIX systems, 20 Macs, and 136 PCs. All computers are connected to a common high-speed switched data network which supports Ethernet; Fast-Ethernet and Gigabit-Ethernet also are supported. ICESS has a 1000Mb/s connection to the UCSB campus backbone which provides shared access to a 622Mb/s CALREN-2 connection, which in turn provides access to Internet2. The computing environment is based on a network of primarily Compaq Digital and Sun workstations (Alphas and Sun SPARC) as well as two Compaq Digital XP1000 systems each with 1.5GB of main memory and one 500MHz 21264 processor, and an SGI Origin 2000 with 4 300MHz R12000 processors and 5GB of main memory. PC’s with Intel processors and Windows operating systems are the most common desktop computers. The total hard disk storage at ICESS is presently about 17TB. High-performance Fiber Channel and SCSI disk arrays allow participants to add disk storage to the environment in disk-sized increments. Backups of all systems are performed nightly or weekly via a tape robot. Tape archival software allows moving of data sets to and from secondary (disk) and tertiary (tape) storage. There are seven networked printers including a color laser printer and a 36" color ink-jet plotter. A full complement of computational, image processing, statistical, database, graphical, scientific visualization, and animation software are available.

A server dedicated to the TCR-LTER will be incorporated into the ICESS computational facility. The TCR-LTER data base will be maintained on this system and data will be made available to all investigators and the public via the ICESS and campus networks. The system will be maintained (e.g. system and software upgrades, system backups) by personnel in the IM group.

Approach and Metadata Standards

The TCR-LTER will use ASCII text for all long-term data table and metadata storage, with the exception of original binary formats such as raster images. Each research group will implement the necessary discipline-specific protocols for data collection and archiving. The groups will work closely with the IM group and the ICESS Systems Group to implement the data handling protocols as data flow from the field onto the TCR-LTER fileserver.

Figure S.1 shows how data from field instruments and manually collected data sheets are first downloaded or entered on local workstations (including those at the Gump Research Station), and are immediately copied to the fileserver for archive and backup. The server is accessed via a web client, Windows SMB client, and Appletalk client or via command line or graphical SSH clients. Data initially will be stored in ‘internal’ (TCR-LTER only) working folders and will be processed according to QA/QC protocols as specified by the research groups. Once processed, data will be copied to ‘internal’ final folders, where they will be used in analyses. Processed data will also be ingested into a desktop data management application called Morpho, which is being developed at the National Center for Ecological Analysis and Synthesis (NCEAS) at UCSB. Morpho is being used successfully by the Santa Barbara Coastal (SBC) LTER site. The data will be documented in the Ecological Metadata Language (EML), which is a simple, comprehensive text-based metadata syntax implemented in XML (an Internet-standard markup language). Once documented in Morpho, the data/metadata packages will be uploaded into the TCR-LTER data catalog which will reside on a dedicated server. Certain documents, such as protocol manuals, that may be too large to convert to EML, will be placed in ‘external’ final working folders that will be accessible via the TCR- LTER web page (referenced within EML data packages).

Data that will be used in analyses, but are not directly collected by LTER researchers, such as publicly available remote sensing data, will be pre-processed for use and the products documented in the data catalog along with the other primary datasets. URL pointers to the original data will be included in the documentation of these data sources.

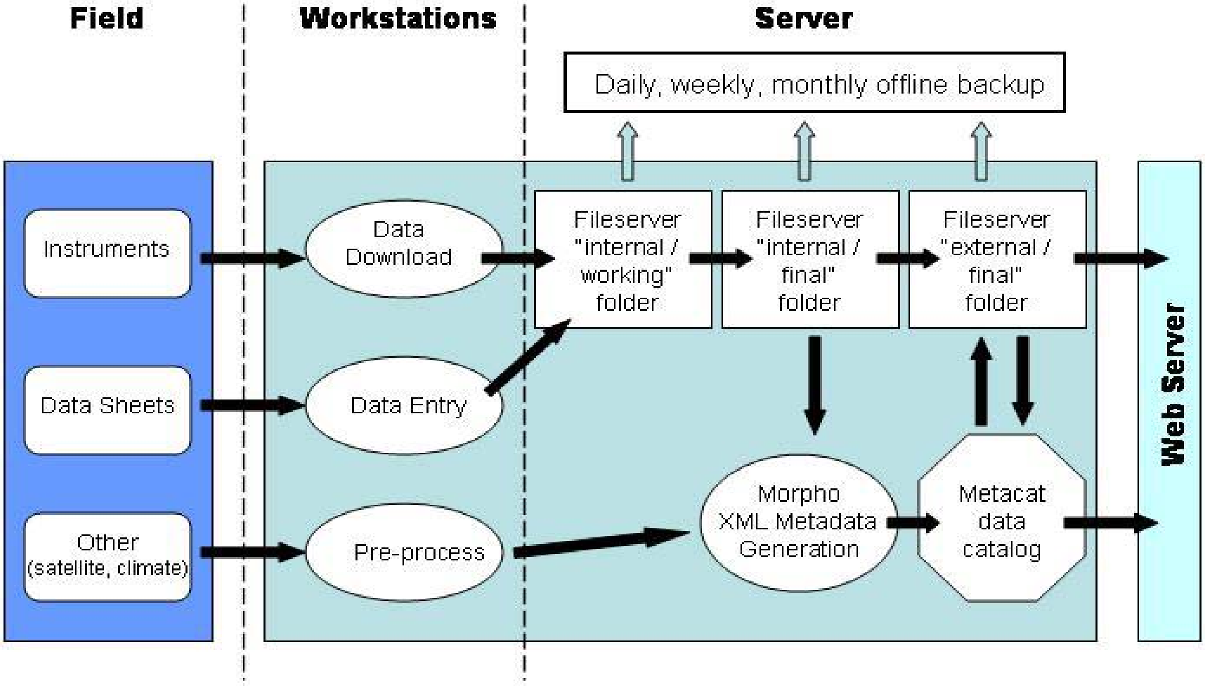
We also plan to integrate an EML analysis tool called Monarch, which is being developed by NCEAS. The advantage of such a tool is that disparate data can be integrated and analyzed using common analytical environments (e.g., SAS, Matlab) for the processing.

To enhance efficiency of data collection and entry, we will explore the use in the field of handheld computers that are linked to a metadata database. The NSF-funded Jalama project (involving NCEAS, SBC-LTER and PICSO) is developing software for handheld computers that will allow researchers to create customized data entry forms and to synchronize their data to the larger data catalog without intermediate steps. We will implement these products when they become available.

The TCR-LTER data catalog will be a web-based server that will respond to HTTP and HTTPS requests, and will be able to store both data and XML-based metadata. The server software is being developed actively at NCEAS and used by the SBC LTER, and will be provided to help research stations develop, store and serve structured metadata and data for view or for more advanced machine processing and analyses. The interaction between the web and/or desktop-based clients and the Netacat server will be implemented as a java servlet that dispatches various requests to the software subsystems. The subsystems will comprise a series of java classes that perform discrete tasks, such as querying, inserting, updating and deleting records in the SQL database, where the metadata are stored. The system is built in a modular fashion such that back-end database technologies may be swapped out.

An immediate advantage of storing EML metadata in the catalog arises from the ease of transformation into web pages that can be viewed on the TCR- LTER web site. We will use a built-in XSLT processor in the metadata catalog to provide customized web pages that will expose the contents of the data catalog to the public. The replication subsystem also will be used to synchronize the TCR- LTER data packages with the LTER Network Office to participate in projects involving network-wide synthesis.

Figure S.1. Proposed flow of data from the Tahitian Coral Reef LTER from field sampling and publicly accessible data sources, to the LTER server and data catalog, where data and metadata will be accessible via the Tahitian LTER web site.



OUTREACH AND EDUCATIONAL ACTIVITIES

The TCR-LTER Education and Outreach program will consist of three components: (1) supporting education programs for the local communities in French Polynesia, (2) a K-12 Schoolyard Program, and (3) providing integrative postdoctoral, graduate, undergraduate student training.

1. Local Community Education Program – A number of our outreach efforts will take place in French Polynesia. The PIs and researchers will work with local educators to translate the goals and findings of the program to the public and school education programs (see attached letter from Ms. Hinano Teavai, Coordinator of the Atitia Center). The Gump Research Station has developed the Atitia Center on its grounds for this purpose. One of the primary functions of the Atitia Center is to provide an infrastructure that visiting scientists can utilize to disseminate the results of their research to the local community. Through a partnership with a Tahitian non-profit association called Te Pu 'Atiti'a, which is largely made up of local educators (including many school teachers) and traditional experts, scientists can overcome the linguistic and cultural barriers to communicating about their science with the local community. This partnership provides scientists with a well-supported education program that works to meet the goal of the Atitia Center of fostering "interaction and exchange, enabling students and researchers to learn from the local community, to contribute scientific knowledge, and to help protect Polynesia's biocultural heritage." The Atitia Center also is developing a comprehensive website as an education and conservation resource that not only will serve the people of French Polynesia, but also can help us target the large Polynesian and Pacific Island communities in California and other parts of the United States. Additionally, the Gump Research Station has a small internship program for Tahitian university students. These students join research teams at the Station for periods of a few weeks or months, usually during school holidays. We plan to expand these efforts.

2. K-12 Schoolyard Program – We will collaborate with successful K-12 programs at UCSB and CSUN to offer a Schoolyard Program, with a focus on teacher professional development. We will use a residential summer institute model, which has proven effective and provides a way to recruit teachers from more distant school districts. Our goal will be to recruit teachers from the 5 counties that bridge UCSB and CSUN, with a particular focus on teachers from underserved and low-performing schools. Our institutes are designed with these findings in mind: (1) that sustained experiences are most likely to have greatest impact, (2) that a focus on pedagogical content knowledge — teaching practices in specific content domains — active learning by participants, and integration into the daily life of the school are more likely to produce enhanced knowledge and skills, and (3) that collective participation (*e.g.*, teachers from a similar discipline, grade, or school) and coherent professional development activities support real change in teaching practices (Garet et al. 2001). Institutes will be followed by academic year workshops to maintain an on-going focus with our community of teachers (Table S.1).

3. Undergraduate and Graduate Student Education – The PIs and researchers will use this project as a catalyst for developing an advanced education and research training program. In addition to the traditional opportunities to develop and hone research skills, students will learn fundamental skills necessary to organize and carry out interdisciplinary, collaborative research.

The first step will be to recruit students into the research group. We will emphasize recruitment and retention of underrepresented students by providing a support structure and developing role models. The University of California, Santa Barbara (UCSB) and California State University, Northridge (CSUN) have relatively large Hispanic, Native American and Pacific Island student populations (Fig. S.2); CSUN is designated a "Hispanic-serving Institution." We will consult various minority support offices (e.g., Educational Opportunities Program, Academic Achievement Program) to advise and support these efforts. The goal is to recruit two undergraduate students per year from each campus for two years of support each. We will also support at least four graduate students each year (two at UCSB and two at CSUN). This will maintain at least one year of overlap between outgoing and incoming students to enhance student community development.

We will promote interaction among students from the two campuses through frequent workshops and seminars. Workshops and seminars will be held on both campuses to encourage "cross-fertilization" of research ideas and provide exposure of graduate students to contrasting academic systems (i.e., UCSB versus CSUN) with a view to: a) fostering recruitment from CSUN (M.S. program) to UCSB (Ph.D. program), and b) providing exposure to a variety of career paths as an effective and important part of graduate training. These experiences will develop a community of students working on related projects within the LTER. In addition, we will develop a webpage specifically for our students to communicate and share data. We intend for this training program to promote recruitment of students through our graduate programs (e.g., undergraduate student applicants to the CSUN M.S. and UCSB Ph.D. programs; development of postdoctoral opportunities).

Ultimately, this component is based on the idea that students need role models and training in every aspect of science, including research and mentoring. The structure of this component is based on collaborative learning. Outwardly, the hierarchy is based on position: undergrad student, graduate student (Master's, Ph.D.), postdoctoral associate, and faculty member. However, project members of various positions will be required to train each other, which is an empowering activity that increases learning. Unlike traditional pedagogy, the use of collaboration has been demonstrated to enhance learning and retention, particularly in minority students (Berry 1991). This approach also develops skills in teamwork, effective communication and valid persuasion; in short, necessary skills for a successful science career. This model will be explicit in that the students and post-docs will conduct their research in collaborative units, with individuals from various levels having specific research and training responsibilities including (but not limited to) personnel within the LTER program and the local community in Moorea.

In recent years there has been a growing emphasis on the need to conduct collaborative research to solve complex problems. Gibbons et al. (1994) suggest that most areas of research are growing more interdisciplinary and team-oriented. Indeed, at the national level there has been a focus on understanding the elements of successful collaborations in order to perpetuate international research agendas. Calls for collaborative, interdisciplinary research are being made by panels such as the Advisory Committee for Environmental Research and Education (Pfirman et al. 2003). Further, the success of programs such as the National Center for Ecological Analysis and Synthesis (NCEAS) and support of programs such as NSF's *Biocomplexity in the Environment* demonstrate the synergies that can be achieved through collaboration. However, despite this emphasis on collaborative research, universities have had a difficult time adopting this vision of the future of science. Administrations struggle with developing mechanisms that promote inter-departmental collaborations and recognize multi-investigator projects and their products, while science education programs still emphasize individual, or cooperative, research at best. This project will develop curriculum elements that focus specifically on understanding and developing the skills that enhance collaboration, and putting these new found skills to practice in integrative, interdisciplinary projects.

The PIs will develop workshops that focus on skill development and understanding collaboration technologies. We will invite social science researchers to present seminars on current research in science collaboration (e.g., Ellen Gotesdiener). We will focus on the principles of building collaborations as defined by the model of Mattessich and Monesy (1992) (e.g., vision, structure, communication) and on skills such as group dynamics, conflict resolution and consensus building. As a capstone experience for graduate students and postdocs, we will engage teams in NCEAS-model working groups that will focus on particular themes relative to our research (e.g., population dynamic models). In addition to the theoretical underpinnings of successful collaborations, we will focus on collaboration technologies. These will include telepresence and videoconferencing, secure and reliable communication protocols, and information sharing tools. Workshops will provide hands-on practice with these tools and project participants will incorporate them into meetings, data sharing efforts and other communications.

Table S.1. Annual schedule for the UCSB/CSUN teacher professional development program.

Summer	(1) Teachers engage in the research program with LTER researchers through a residential RET program (2) teachers participate in curriculum development workshops that focus on topics related to LTER research and match state science standards, such as understanding energy transfer through ecosystems.
Fall	Teachers implement curriculum in their classrooms, LTER researchers visit classrooms, teachers conduct curriculum evaluations through on-going active research projects in the classroom.
Spring	Teachers disseminate completed curriculum modules through local workshops, regional and national science teachers conferences (e.g. National Science Teachers Association – NSTA), and at the National Marine Educators Association (NMEA) meetings.

Figure S.2. Undergraduate minority enrollment figures: **(top)** CSUN minority enrollment, **(bottom)** UCSB minority enrollment.