OCS Study
BOEMRE 2010-05

Multi-Agency Rocky Intertidal Network (MARINe) Study of Rocky Intertidal Communities Adjacent to OCS Activities – Final report (2007-2010)

Final Technical Summary
Final Study Report

U.S. Department of the Interior
BOEMRE Bureau of Ocean Energy Management, Regulation and Enforcement
Pacific OCS Region

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by

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Disclaimer

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FINAL TECHNICAL SUMMARY

STUDY TITLE: "Multi-Agency Rocky Intertidal Network (MARINe) Study of Rocky Intertidal Communities Adjacent to OCS Activities"

REPORT TITLE: Multi-Agency Rocky Intertidal Network (MARINe) Study of Rocky Intertidal Communities Adjacent to OCS Activities - Final report (2007-2010)"

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BACKGROUND

Oil and gas activities, especially the tankering of oil along the California coast and the extraction of oil from OCS activities, raise the possibility of an oil spill or other impact to coastal resources. Population monitoring of coastal biota in central and southern California provide baseline information in case an event such as a spill damaged these resources. BOEMRE initiated the formation of a long-term monitoring program, the Multi-Agency Rocky Intertidal Network, MARINe, in 1997, which now has 32 Federal, State and local agency, University and private partners and monitors 120 rocky shore sites. Through this study, BOEMRE funds biannual monitoring at 24 established rocky intertidal sites along the California mainland adjacent to OCS operations. The study also funds operation and maintenance of the shared MARINe database, and coordination of the MARINe committees.

OBJECTIVES

The primary objective for this research is to contribute to the ongoing monitoring program that provides a basis for determining if change in rocky shoreline communities adjacent to producing OCS facilities can be attributed to producing operations or accidents from OCS facilities. The second objective is to provide an ecological context through monitoring so as to understand the natural and anthropogenic changes to these communities that have occurred in the Southern California Bight since the OCS program was initiated. This latter objective is based on a collaboration between MARINe and other groups (especially the Partnership for Interdisciplinary Study of Coastal Oceans (PISCO)) and includes the collection of additional biodiversity data and comparison to comparable historic data (using matching funds). Additional objectives included oversight of a concurrent database process and publication of metadata for the BOEMRE-funded long-term data set.

DESCRIPTION:

The work completed in the period 2007-2010 employed methodologies consistent with the previous MARINe projects in order to maximize comparability among project results. The methodological details for these projects can be found in Engle (2005 and www.marine.gov), and are summarized below.

To accomplish the first objective, target species at 24 established rocky intertidal sites along the mainland coast of Southern and Central California adjacent to producing platforms were monitored spring and fall.

Target species include: mussels (*Mytilus californianus*), barnacles (*Chthamalus* spp., *Balanus glandula* and *Pollicipes polymerus*), anemones (*Anthopleura elegantissima*), algal species including *Endocladia muricata*, *Hesperophycus harveyanus*, *Silvetia compressa*, *Mazzaella* spp., *Mastocarpus papillatus*, surfgrass (*Phyllospadix scouleri/torreyi*), motile invertebrates such as owl limpets (*Lottia gigantea*), black abalone (*Haliotis cracherodii*) and sea stars (*Pisaster ochraceus*). Mussels, barnacles, anenomes and algal species were photographed in fixed rectangular plots and scored in the lab or field (barnacles at some sites) by scoring species under 100 points on each slide. Five replicate plots per target species were photographed at each site where the plots occurred. Surfgrass cover was estimated using a point contact method along 10 m transects. Owl limpets were measured and counted in 5 replicate, 1-meter circular plots at each site where the plots occurred. Abalone were counted and measured in 3 replicate irregular plots. Sea stars were counted, measured and classed by color in either 2 meter wide, 10 m long band transects or irregular plots, depending on the habitat. In many of the target species plots we also sampled the associated motile species. To optimize future environmental impact assessments, sites have been established systematically over a broad geographic range and each species is monitored at several sites within that range. This study also included overall coordination of MARINe, including facilitating meetings with the MARINe Steering Committee, Data Panel, and Science Panel and coordinating use of the data in collaborative projects. A large MARINe database is also populated and maintained for the entire network through this Cooperative Agreement.

Dr. Pete Raimondi, the Project Manager, coordinated the study, and specifically oversaw monitoring in San Luis Obispo and northern Santa Barbara County sites. Dr. Steve Murray and Dr. Jayson Smith at California State University, Fullerton conducted the monitoring in Orange County. Dr. Rich Ambrose at UCLA conducted companion monitoring for southern Santa Barbara and Los Angeles Counties. Dr. Jack Engle at the UC Santa Barbara coordinated MARINe efforts, particularly with regards to protocol standardization and documentation. In addition, the BOEMRE Pacific Regional Intertidal Survey and Monitoring (PRISM) Team participated in the sampling, and other program functions to assure continued coordination with BOEMRE was maintained.

SIGNIFICANT CONCLUSIONS:

Ongoing monitoring of the black abalone documented the continuing decline of the species in much of its range. Additional studies coupled to the MARINe monitoring were carried out to determine the extent of the critical habitat for the species. These two data sets were combined to estimate the population size of Black abalone. These results were critical to the listing of the species as endangered.

MARINe monitoring data was used by the State of California to aid in the Marine Life Protection Act design of the Marine Protected Area (MPA) network for southern California. Intertidal datasets were used to delineate the biogeographic regions and optimal sizes of intertidal MPA's were also calculated based on MARINe datasets.

MARINe datasets were the foundation of the assessment of potential impacts to the State designated Areas of Special Biological Significance.

STUDY RESULTS:

During the course of the performance period for this contract all 24 sites were sampled, usually twice per year (Table 2). Both sessile and motile species were sampled and sampling was generally uneventful. Fourteen target species were sampled across the project sites and in many of these plots, motile species were also sampled. During this period no additional sites were set up using direct BOEMRE funding, but 38 sites were set up using co-funding from the State of California (MPA and ASBS funding) and the U.S. Fish and Wildlife Service.

During this period MARINe protocols were accepted as the first approved monitoring protocol for the U.S. National Park Service monitoring program (for Redwoods National

Park), and these protocols are now being used as the basis of monitoring programs in Park Service areas on the east coast.

In terms of the biological communities sampled, the major result is the continued decline in the black abalone. The decline during this period was more muted than in the past, but still present. Importantly recruitment of new individuals still has not occurred at sites affected severely by the withering disease. Other species were dynamic but the changes in populations were not outside natural dynamics. We continued to monitor invasive species, but did not note any additional invasions. A full data report covering all MARINe sites will be finished in 2011. This report will be a comprehensive assessment of the entire MARINe region and cover species dynamics at spatial scales from 1000's to 10's of kilometers and temporal scales from seasons to decades. This will be the most comprehensive assessment of a marine ecosystem (rocky intertidal throughout much of the California Current region) ever done.

STUDY PRODUCT(S): Products include annual update of the MARINe database, collection and archival of photos and specimens, 135 conference presentations, 39 peer reviewed papers and posters, and 25 reports. See report and www.MARINe.gov for full listing.

FINAL STUDY REPORT

PART I: INTRODUCTION, OBJECTIVES, AND APPROACH

1.1 Introduction

The central/southern California mainland and Channel Islands seacoasts possess an exceptional diversity of valuable rocky intertidal resources. Major factors contributing to the richness of coastal marine life in this region include their location along the boundary of two major biogeographic provinces (cold-temperate Oregonian and warm-temperate Californian), their high diversity of habitat types, and their exposure to varying local oceanographic conditions. In addition, these rocky intertidal resources are heavily utilized (Thompson et al. 1993), with large human populations concentrated on the coastlines of San Diego, Orange and Los Angeles Counties. Oil and gas activities, especially the tankering of oil along the California coast and the extraction of oil from Outer Continental Shelf (OCS) activities, raise the possibility of an oil spill or other impact to coastal resources. Population monitoring of coastal biota in central and southern California would provide baseline information in case an event such as a spill damaged these resources. This baseline information would be essential for (1) scientific studies investigating the short- and long-term effects of the spill, and (2) natural resource damage assessment. In addition, the monitoring studies would yield important data on population dynamics on a local and regional scale, which could be utilized for more effective resource management as well as provide fundamental ecological knowledge about the dynamics of the systems.

Federal, state and local agencies have recognized the importance of baseline information on coastal ecological resources by funding the establishment of a network of monitoring stations noted above. Of the over 120 established MARINe sites, over half are funded by Federal agencies, (e.g., BOEMRE, The National Park Service), and the balance are funded by private, State, and non-governmental entities. The biological information acquired during these surveys also is incorporated into resource databases hosted by the Multi-Agency Rocky Intertidal Network (MARINe) and Partnership for Interdisciplinary Study of Coastal Oceans (PISCO). This innovative monitoring program was initiated by the Channel Islands National Park in the early 1980's (Davis 1985; Richards and Davis 1988). In 1990, the Cabrillo National Monument in San Diego County began long-term rocky intertidal monitoring (Davis and Engle 1991). Monitoring in Santa Barbara County began in 1992 with a project funded jointly by the Bureau of Ocean Energy Management (BOEMRE), formerly the Minerals Management Service (MMS), which funded monitoring of intertidal and subtidal resources (Ambrose et al. 1992a, b), and the County of Santa Barbara, which funded monitoring of wetland resources (Ambrose et al. 1993). In 1994, it was expanded by the California Coastal Commission (CCC) to include the northern Channel Islands (particularly Santa Cruz Island) and Ventura and Los Angeles Counties (Engle et al. 1994). The CCC projects include monitoring of subtidal, rocky and sandy intertidal and, for Los Angeles/Ventura Counties, wetland resources. Although the monitoring network is principally motivated by oil and gas activities, the information it generates provides valuable information about the status and trends of the biological resources of the region, similar to the Environmental Protection Agency (EPA)'s Environmental Monitoring & Assessment Program (EMAP) but on a finer spatial scale. The National Research Council has also emphasized the value of coordinated regional monitoring such as proposed here (NRC 1990a, b).

Nearshore coastal resources can be divided into three general habitat types: intertidal, subtidal, and coastal wetland. All three habitat types could be impacted by an oil spill. Numerous studies have documented major oil spill impacts on rocky intertidal regions (see Foster et al. 1986 for review). Impacts to subtidal habitats are likely to be less (and would certainly be less conspicuous). Coastal wetlands are particularly susceptible to damage from spilled oil; however, many wetlands along the southern California coast are isolated from the open sea during part of the year, or could be protected by booming or diking should a spill occur.

Central and Southern California Rocky Intertidal Habitats

The extent of rocky shoreline varies substantially in central and southern California (Ambrose et al. 1989). The northern section of the region and the Channel Islands are predominantly rocky (Table 1). San Luis Obispo County has the most extensive stretch of rocky shores (54 mi, or 58% of its coastline) in the region, except for the Channel Islands. Ventura and Orange Counties have the least rocky shoreline, each with 3 miles or 7% of the coastline.

Location	Coastline Length (mi)	Miles Rocky	Miles Sandy	% Rocky	% Sandy
San Luis Obispo Co.	93	54	39	58	42
Santa Barbara Co.*	110	26	84	24	76
Ventura Co.*	41	3	38	7	93
Los Angeles Co.*^	77	26	51	34	66
Orange Co.	41	3	38	7	93
San Diego Co.	76	11	65	14	86
Channel Islands	273	211	62	77	23

* excludes Channel Islands ^ includes harbor breakwaters

Table 1: Extent of rocky and sandy shores for central/southern California. (Mainland data from Littler and Littler, 1979. Island data from Littler and Littler 1980)

The biological communities of the mainland from San Luis Obispo County in the north to Orange County in the south are distinctly different north and south of Point Conception.

San Luis Obispo and Northern Santa Barbara Counties (north of Point Conception)

Rocky intertidal communities to the north of Pt. Conception are well-known for their diverse and relatively pristine biota. The majority of the coast is either privately-owned, owned by the military, or inaccessible and is undeveloped. The natural beauty and coastal resources of this area make it a popular tourist destination, as evidenced by more than 10 State and County Parks and Beaches. A majority of the shore consists of rugged rocky reefs fully or partially exposed to prevailing oceanic swells. Situated at the northern end of the transition zone between southern (Californian) and northern (Oregonian) biota, these intertidal habitats contain a unique mix of species, with warm-temperate species declining and cold-temperate forms increasing in abundance compared with counties to the south. For example, warm-water sea palms (*Eisenia arborea*), rockweed (*Hesperophycus harveyanus*), barnacles (*Tetraclita rubescens, Chthamalus fissus*), and horse mussels (*Brachidontes adamsianus*) are rare or absent, while cold-water sea palms (*Postelsia palmaeformis*), rockweed (*Fucus distichus, Pelvetiopsis limitata*), barnacles (*Balanus glandula, Chthamalus dalli*), and horse mussels (*Septifer bifurcata*) appear or increase in abundance in SLO county. Black abalone (*Haliotis cracherodii*) populations have crashed due to disease, during the period of MARINe monitoring.

The rich marine communities of this region are vulnerable to oil spills or other oil and gas operations impacts, primarily from major coastal tanker traffic, but also from terminal operations at Estero Bay, onshore pipeline breaks, and possible future oil exploration leases. Spills from OCS platforms also pose a threat. The Torch Platform Irene pipeline oil spill in 1997 landed on shores in this region. In addition, other anthropogenic impacts are vastly increasing, particularly those related to increases human access to shores that were until recently only reachable via private ranches. We have noted huge increases in public presence at sites throughout the region, accompanied by harvest and trampling. Only ongoing monitoring is effective at separating such impacts from those that could be linked to oil operations.

Rocky coast flora and fauna in this region remain largely unstudied except for MARINe studies, those done by the PISCO program, impact surveys associated with the Diablo Canyon Nuclear Power Plant located north of Avila Beach (North et al. 1989, Tenera Environmental 1988a, b, 1994) and research on seasonal and successional variation in intertidal community structure conducted at 2 sites (Point Sierra Nevada and Diablo Canyon) (Kinnetic, 1992). The ongoing Diablo Canyon surveys, initiated in the 1970's, represent an excellent time series for this one area. The seasonal and successional studies at Point Sierra Nevada and Diablo Canyon were funded by BOEMRE, formerly the Minerals Management Service (MMS), during 1985-1991, and currently one of the MARINe sites is at Point Sierra Nevada, thus extending the period of sampling to 2010.

Southern Santa Barbara, Ventura, Los Angeles and Orange Counties (south of Pt. Conception)

This region is prominent in the distribution of rocky intertidal organisms because it is bordered by Point Conception, an important biogeographical transition area. Although there is considerable overlap, there are distinct differences between the organisms north and south of Point Conception (Murray and Littler 1981, Ambrose et al., 1992a, b). For example, seaweed communities north of Point Conception are characterized by species such as *Laminaria*, lean brown algae and large, fleshy red algae, and by greater biomass, whereas communities south of the Point are characterized by fucalean brown algae and shorter, more densely branched red algae (Abbott and Hollenberg 1976).

Concerns about the impact of oil spills in this region stem from transport by offshore tanker and onshore pipeline, production platforms, and terminal operations. Natural oil seeps are prominent features, especially at Point Conception. Previous studies in the region include work by PISCO, Littler and colleagues at Coal Oil Point and Government Point (Littler 1979), funded by BOEMRE, and Kinnetics at Government Point.

1.2 Objectives

The primary objective for this research was to contribute to the ongoing monitoring program that provides a basis for determining if change in rocky shoreline communities adjacent to producing OCS facilities can be attributed to producing operations or accidents from OCS facilities. The second objective was to provide an ecological context through monitoring so as to understand the natural and anthropogenic changes to these communities that have occurred in the Southern California Bight since the OCS program was initiated. This latter objective is based on collaboration between MARINe and other groups (especially PISCO) and includes the collection of additional biodiversity data and comparison to comparable historic data (using matching funds). Additional objectives included oversight of a concurrent database process and publication of metadata for the BOEMRE-funded long term data set.

1.3 Approach

The work completed in the period 2007-2010 employed methodologies consistent with the previous MARINe projects in order to maximize comparability among project results. The methodological details for these projects can be found in Engle (2005 and www.marine.gov), and are summarized below.

Target Species Monitoring

To accomplish the first objective, target species at 24 established rocky intertidal sites along the mainland coast of Southern and Central California adjacent to producing platforms were monitored spring and fall (Table 2, Figure 1).

Site Name	SiteID	North/South Order	Group	Principal Investigator	Seasons Sampled
Point Sierra Nevada	PSN	1	UCSC	Pete Raimondi	2007 Spring to 2010 Fall
Piedras Blancas Lighthouse	PBL	2	UCSC	Pete Raimondi	2007 Spring to 2010 Fall
Rancho Marino Reserve	RMR	3	UCSC	Pete Raimondi	2007 Spring to 2010 Fall
Cayucos	CAY	4	UCSC	Pete Raimondi	2007 Spring to 2010 Fall
Hazards	HAZ	5	UCSC	Pete Raimondi	2007 Spring to 2010 Fall
Shell Beach	SHB	6	UCSC	Pete Raimondi	2007 Spring to 2010 Fall
Occulto	OCC	7	UCSC	Pete Raimondi	2007 Spring to 2010 Fall
Purisima	PUR	8	UCSC	Pete Raimondi	2007 Spring to 2010 Fall
Stairs	STA	9	UCSC	Pete Raimondi	2007 Spring to 2010 Fall
Boathouse	BOA	10	UCSC	Pete Raimondi	2007 Spring to 2010 Fall
Government Point	GPT	11	UCSC	Pete Raimondi	2007 Spring
Alegria	ALEG	12	UCLA	Rich Ambrose	2007 Spring to 2010 Fall
Arroyo Hondo	ARHO	13	UCLA	Rich Ambrose	2007 Spring to 2010 Fall
Coal Oil Point	COPT	14	UCLA	Rich Ambrose	2007 Spring to 2010 Fall
Carpinteria	CARP	15	UCLA	Rich Ambrose	2007 Spring to 2010 Fall
Mussel Shoals	MUSH	16	UCLA	Rich Ambrose	2007 Spring to 2010 Fall
Old Stairs	OLDS	17	UCLA	Rich Ambrose	2007 Spring to 2010 Fall
Paradise Cove	PCOV	18	UCLA	Rich Ambrose	2007 Spring to 2010 Fall
Whites Point	WHPT	19	UCLA	Rich Ambrose	2007 Spring to 2010 Fall
Point Fermin	PTFM	20	UCLA	Rich Ambrose	2007 Spring to 2010 Fall
Crystal Cove	CRCO	21	CSUF	Steve Murray	2007 Spring to 2010 Fall
Shaws Cove	SHCO	22	CSUF	Steve Murray	2007 Spring to 2010 Fall
Treasure Island	TRIS	23	CSUF	Steve Murray	2007 Spring to 2010 Fall
Dana Point	DAPT	24	CSUF	Steve Murray	2007 Spring to 2010 Fall

Table 2: Sites sampled from north to south, group and Principle Investigator (PI) responsible for sampling and the seasons that were sampled during the contractual period.

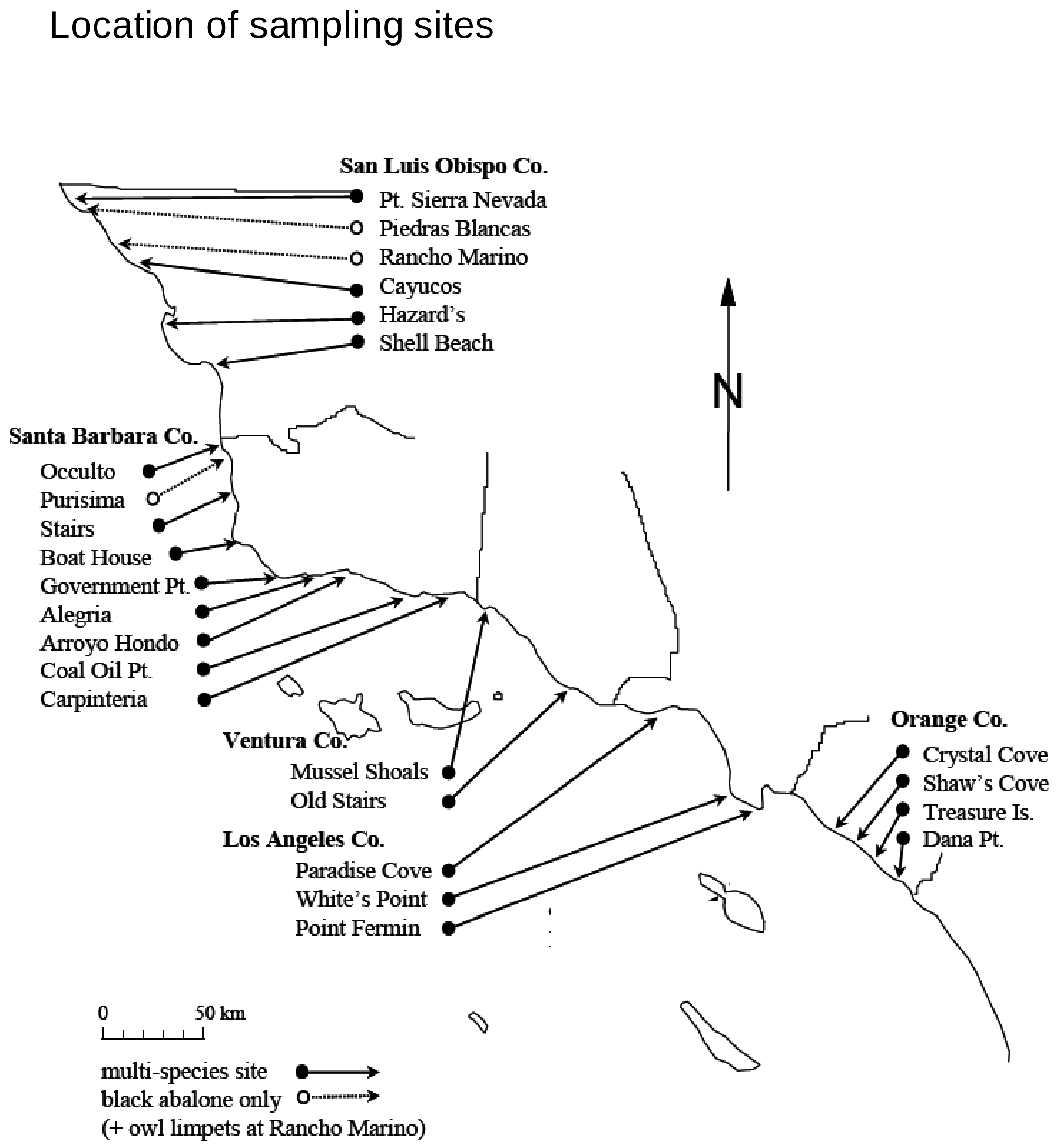

Figure 1: Location of Sampling Sites

Target species include: mussels (*Mytilus californianus*), barnacles (*Chthamalus* spp., *Balanus glandula* and *Pollicipes polymerus*), anenomes (*Anthopleura elegantissima*), algal species including *Endocladia muricata*, *Hesperophycus harveyanus*, *Silvetia compressa*, *Mazzaella* spp., *Mastocarpus papillatus*, surfgrass (*Phyllospadix scouleri/torreyi*), motile invertebrates such as owl limpets (*Lottia gigantea*), black abalone (*Haliotis cracherodii*) and sea stars (*Pisaster ochraceus*). Table 3 shows the target species at each of the sites sampled. Table 4 shows the plots in which motile species were also sampled. Analysis following the 167 bbl. "Torch spill", an OCS pipeline spill from the Platform Irene pipeline, showed that it was possible to detect change in percent cover of barnacles and mussels as small as 8-15% using this fixed plot sampling protocol. Importantly, it was also possible to differentiate between natural changes such as the El Nino storms and the effects of the oil spill (Raimondi et. al, 1999). It is vital that the monitoring protocol is in sufficient detail to address these low-level changes.

Mussels, barnacles, anenomes and algal species were photographed in fixed rectangular plots and scored in the lab or field (barnacles at some sites) by scoring species under 100 points on each slide. Five replicate plots per target species were photographed at each site where the plots occurred. Surfgrass cover was estimated using a point contact method along 10-meter long transects. Owl limpets were measured and counted in five replicate, 1-meter circular plots at each site where the plots occurred. Abalone were counted and measured in three replicate irregular plots. Sea stars were counted, measured and classed by color in either 2-meter wide, 10-meter long band transects or irregular plots, depending on the habitat. In many of the target species plots, we also sampled the associated motile species (Table 4). To optimize future environmental impact assessments, sites have been established systematically over a broad geographic range and each species is monitored at several sites within that range.

Monitoring of the long-term sites was usually done in Fall and Spring each year, although the motile species in target species plots were sometimes sampled only once per year (see Table 4). There can be considerable seasonal changes in the rocky intertidal community, especially after stormy winters and hot summers. Two samples per year adequately track these communities. October or November is usually the first period after summer with low tides during the daytime (which greatly improve efficiency of sampling and safety), and is appropriate for determining the post-summer community. March or April is an appropriate time to determine the post-winter community, and there are once again low tides during the daytime.

	Target Species													
Site Name	anthopleura	chthamalus/balanus	endocladia	haliotis	hespero-phycus	lottia	masto-carpus	mazzaella	mytilus	pisaster	pollicipes	postelsia	recovery	silvetia
Point Sierra Nevada		X		X	X		X	X	X	X		X		X
Piedras Blancas Lighthouse		X		X			X		X	X		X		X
Rancho Marino Reserve				X		X								
Cayucos		X	X	X	X	X			X	X				X
Hazards		X	X			X		X	X	X				X
Shell Beach		X	X				X		X	X				X
Occulto		X	X						X	X				
Purisima				X										
Stairs		X	X	X		X			X	X			X	X
Boathouse	X	X	X	X		X			X	X				X
Government Point		X	X	X		X			X	X	X			X
Alegria	X	X				X			X	X	X			
Arroyo Hondo		X							X	X				
Coal Oil Point	X								X					
Carpinteria	X	X				X			X	X	X			
Mussel Shoals	X	X				X			X	X				
Old Stairs	X	X	X			X			X	X				
Paradise Cove		X	X			X			X	X				
Whites Point		X	X			X			X	X				
Point Fermin		X				X			X	X				X
Crystal Cove		X				X			X	X				X
Shaws Cove		X	X			X			X	X				X
Treasure Island		X							X	X				X
Dana Point		X				X			X	X				X

Table 3: Target species sampled (X) at each of the 24 sample sites.

	Target Species								
Site Name	chthamalus / balanus	endocladia	hespero-phycus	mastocarpus	mytilus	pollicipes	recovery	silvetia	Motile Sampling Notes
Crystal Cove	X				X			X	
Dana Point	X				X			X	
Shaws Cove	X	X			X			X	
Treasure Island	X				X			X	
Piedras Blancas Lighthouse	X			X	X			X	Spring sampling only
Alegria	X				X	X			Spring sampling only
Arroyo Hondo	X				X				Spring sampling only
Carpinteria	X				X	X			Spring sampling only
Coal Oil Point					X				Spring sampling only
Mussel Shoals	X				X				Spring sampling only
Old Stairs	X	X			X				Spring sampling only
Paradise Cove	X	X			X				Spring sampling only
Point Fermin	X				X			X	Spring sampling only
Whites Point	X	X			X				Spring sampling only
Boathouse	X	X			X			X	
Cayucos	X	X	X		X			X	
Government Point	X	X			X			X	
Hazards	X	X			X			X	
Occulto	X	X			X				No Fall 2007 sampling
Point Sierra Nevada	X		X		X			X	
Shell Beach	X	X		X	X			X	
Stairs	X	X			X		X	X	No Fall 2007 sampling

Table 4: Target species plots in which motile organisms were sampled

Depending on the size of the site and the number of target species being monitored, one pair to three pairs of biologists was needed to collect the field data. The majority of sites needed four to five trained biologists to complete the work on a given tide. Pacific Region Intertidal Survey and Monitoring (PRISM) Team, formerly MMS Intertidal Team (MINT) biologists assisted in the collection of the field data at as many as 20 of the sites depending on tidal cycles. Travel to and from sites benefited from cost sharing since several sites can be surveyed during one tide cycle.

Protocols used to collect the data were standardized, coordinated with other members of MARINe, and were not altered without prior approval of BOEMRE. A base protocol was standardized across the Bight among MARINe members and was maintained at each site; additional protocols needed to address site specific problems or answer species-specific questions were sometimes added with BOEMRE approval. Additional protocols which did not add field costs overall were accommodated in order to address these important research questions, so long as this was coordinated properly with MARINe members.

This collection of field data was carried out by the University of California, Santa Cruz (UCSC), University of California, Los Angeles (UCLA), and California State University, Fullerton (CSUF) (see Table 2).

Coordination—Internal and with MARINe

Since several teams of biologists were needed to collect data at over 120 established sites (including the 24 covered in this grant proposal), coordination among field teams was essential to ensure that the data collected was of the highest quality and is comparable across sites. Therefore, strong coordination was needed between the Principal Investigators (PI)'s to ensure continuity since the tasks were inherently integrated between Universities. This coordination included regular meetings, email, phone calls and joint participation in the field. This ensured that individual PI's are not inadvertently making changes in protocols or data processing which affect the other PI's.

Strong coordination was also needed between BOEMRE and MARINe to ensure that BOEMRE was providing data in a timely fashion to MARINe and that MARINe products directly met the needs of the scientists, including the BOEMRE PI's. BOEMRE committed to providing a MARINe coordinator to that end. The duties of the coordinator included:

1. Facilitating the development of the database by:
    a. Acting as a liaison between the database consultant and MARINE researchers in developing timely responses to database questions.
    b. Coordinating with the BOEMRE researchers in particular and MARINE researchers in general to ensure their data and metadata inputs are complete and timely.

   c. Providing a broad range of knowledge regarding the MARINE sites and technical issues to the database consultant to ensure that the database will be useful to researchers when it is completed.
2. Organizing and moderating biannual Steering Committee, Science Panel and Database Panel meetings for MARINe.
3. Providing ongoing coordination with the MARINe committee representatives and organizations outside MARINe to facilitate continued long-term funding of MARINe sites.
4. Working with MARINe to develop automated standardized field datasheets.
5. Working with MARINe to reach agreement and develop procedures which promote timely release of data to the public.

These tasks were done at all campuses but the responsibility for coordination was centered at the University of California, Santa Barbara (UCSB).

Data management

Data management was overseen at UCSC. Duties included administering data in the MARINe (access) database. All campuses were responsible for uploading data using data forms, but no alterations to the database were be made without approval from the data administrator. Data were accessible via the Microsoft Access relational database management system interface, and revisions were made approximately twice per year. Data are available to all agencies and interested parties that make specific requests.

Project management

The UCSC portion of the program was managed by the Principal Investigator, Dr. Pete Raimondi. Dr. Raimondi has been a Principal Investigator of the BOEMRE-funded rocky intertidal inventory project since its inception and has been responsible for data analysis of the project for the past ten years. Dr. Raimondi was responsible for overseeing financial aspects of the project, and in particular was responsible for ensuring completion of project objectives and deliverables. This was done, in part, through coordination meetings and conference calls. However the main means of ensuring performance was through the yearly workshops where all PI’s get together along with staff to review the status of the project.

Because this proposal is part of an overall coordinated monitoring program, the work was closely coordinated with other aspects of that program. Overall coordination was led by Dr. Steve Murray and Jayson Smith at CSUF, who conducted similar monitoring in Orange County. Dr. Rich Ambrose at UCLA conducted companion monitoring for southern Santa Barbara and Los Angeles Counties. Dr. Jack Engle at the UCSB coordinated MARINe efforts, particularly with regards to protocol standardization and documentation. In addition, the BOEMRE PRISM Team participated in the sampling, and other program functions to assure continued coordination with BOEMRE was maintained.

1.4 Significant Conclusions

Ongoing monitoring of the black abalone documented the continuing decline of the species in much of its range. Additional studies coupled to the MARINe monitoring were carried out to determine the extent of the critical habitat for the species. These two data sets were combined to estimate the population size of black abalone. These results were critical to the listing of the species as endangered.

MARINe monitoring data was used by the State of California to aid in the Marine Life Protection Act design of the Marine Protected Area (MPA) network for southern California. Intertidal datasets were used to delineate the biogeographic regions and optimal sizes of intertidal MPA's were also calculated based on MARINe datasets.
MARINe datasets were the foundation of the assessment of potential impacts to the State designated Areas of Special Biological Significance (ASBS).

1.5 Study Results

During the course of the performance period for this contract all 24 sites were sampled, usually twice per year (Table 2). Both sessile and motile species were sampled and sampling was generally uneventful. Fourteen target species were sampled across the project sites and in many of these plots, motile species were also sampled. During this period no additional sites were set up using direct BOEMRE funding, but 38 sites were set up using co-funding from the State of California (MPA and ASBS funding) and the U.S. Fish and Wildlife Service.

During this period MARINe protocols were accepted as the first approved monitoring protocol for the U.S. National Park Service monitoring program (for Redwoods National Park), and these protocols are now being used as the basis of monitoring programs in Park Service areas on the east coast.

In terms of the biological communities sampled, the major result is the continued decline in the black abalone. The decline during this period was more muted than in the past, but still present. Importantly, recruitment of new individuals still has not occurred at sites affected severely by the withering disease. Other species were dynamic but the changes in populations were not outside natural dynamics. We continued to monitor invasive species, but did not note any additional invasions. A full data analysis report covering all MARINe sites will be finished in 2011. This report will be a comprehensive assessment of the entire MARINe region and cover species dynamics at spatial scales from 1000's to 10's of kilometers and temporal scales from seasons to decades. This will be the most comprehensive assessment of a marine ecosystem (rocky intertidal throughout much of the California Current region) ever done.

1.6 Study Product(s)

Products include the following: continual enhancements to the MARINe Database; launch of a completely revamped public MARINe website, (which includes current news and research); restructuring of the private website (in progress); online availability of all MARINe data on www.piscoweb.org, (including data not previously included in the Access Database); the update of the MARINe Handbook, including updated tables and protocol enhancements; archival of photos and specimens; conference presentations, peer reviewed papers and posters, and reports; and organization and recording of data and info requests. Listed below are products of MARINe during this period; starred items were produced either using BOEMRE funding, using data collected at BOEMRE funded sites, or presented at a BOEMRE funded workshop.

Presentations (2007-2010)

*Ambrose, R. 2007. Oil spill rapid response protocols. MARINe Annual Workshop, San Francisco, CA.

*Ambrose, R. 2007. Public access versus resource protection. MARINe Annual Workshop, San Francisco, CA.

Ammann, K.N. 2010. Long-term rocky intertidal monitoring of Redwood National and State Parks. Presentation for National Park Service Klamath Network Inventory and Monitoring Program-Three Year Program Review.

*Ammann, K.N., C.A. Bell. M.K. George, and P.T. Raimondi. 2009. An overview of the biological sampling used to assess the central California coast marine protected areas – with emphasis on rocky intertidal habitats. Western Society of Naturalists Annual Meeting, Monterey, CA.

*Anderson, D. 2009. Survey team monitoring summary: Northern CA/Oregon. MARINe Annual Workshop, San Francisco, CA.

*Anderson, L. 2009. Survey team monitoring summary: Santa Barbara/San Luis Obispo Counties. MARINe Annual Workshop, San Francisco, CA.

Augyte, S. and F.J. Shaughnessy. 2010. A preliminary floristic analysis of marine intertidal algae from Cape Mendocino, CA to Cape Blanco, OR. Western Society of Naturalists Annual Meeting, San Diego, CA.

*Bell, C. 2007. Digital photo archive - where are we now and where are we headed? MARINe Annual Workshop, San Francisco, CA.

*Bell, C. 2008. Go-kit protocol demonstration and what we learned from the Cosco Busan Oil Spill. MARINe Annual Workshop, San Pedro, CA.

*Bell, C. 2008. Optional protocols revisited. MARINe Annual Workshop, San Pedro, CA.

*Bell, C.A., K.N. Ammann, M.K. George, and P.T. Raimondi. 2009. Assessing the amount of suitable habitat and the population size of black abalone (*Haliotis cracherodii*) from Half Moon Bay to Point Conception. Western Society of Naturalists Annual Meeting, Monterey, CA; Black Abalone Critical Habitat Meeting, Ventura, CA; and MARINe Annual Workshop, San Francisco, CA.

*Bell, C.A., K.N. Ammann, M.K. George, and P.T. Raimondi. 2010. Assessing suitable habitat and the population size of black abalone (*Haliotis cracherodii*) for critical habitat designation. Poster at Western Society of Naturalists Annual Meeting, San Diego, CA.

Bell, Christy. 2007. The importance of community structure and biodiversity surveys to establish baseline data for Marine Reserves. COBI Fishing CO-OP meeting, Isla Natividad, Baja California Sur, Mexico.

*Blanchette, C. 2009. Biodiversity survey overview. MARINe Annual Workshop, San Francisco, CA.

Blanchette, C.A. 2007. Intertidal communities of the CA Channel Islands: ecology and natural history. Western Society of Naturalists Annual Meeting, Ventura, CA.

Blanchette, C.A., P.T. Raimondi, and B. R. Broitman. 2008. Spatial patterns of intertidal community structure across the California Channel Islands and links to ocean temperature. 7th California Islands Symposium, Oxnard, CA.

*Conway-Cranos, L. 2007. Geographic patterns of recovery in intertidal communities. Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) Scientific Symposium. Corvallis, OR.

*Conway-Cranos, L. 2007. Prediction and understanding the recovery of communities: An example from the rocky intertidal. Pacific Ecology and Evolution Conference. Seattle, WA; and Ecological Society of America Annual Conference. San Jose, CA.

*Conway-Cranos, L. 2010. An investigation of the relative importance of mechanisms driving variation in the recovery of mussel beds. Western Society of Naturalists Annual Meeting, San Diego, CA.

*Conway-Cranos, L. 2010. Recovery dynamics in rocky intertidal communities: An experimental evaluation of resilience. Seminar at Friday Harbor Marine Laboratory, University of Washington, WA.

*Conway-Cranos, L.. 2009. Recovery dynamics in rocky intertidal communities: Patterns, mechanisms and simulations. Ecological Society of America Annual Conference, Albuquerque, NM and Bodega Marine Laboratory Seminar.

*Conway-Cranos, L.L. 2008. Facultative interactions as a potential driver for spatial variation in recovery patterns in the California rocky intertidal. Western Society of Naturalists Annual Meeting, Vancouver, BC.

*Conway-Cranos, L.L. 2008. Recovery of intertidal communities: Perspectives from a broad-scale manipulation. MARINe Annual Workshop, San Pedro, CA.

*Cox, K. 2007. MARINe regional sampling update: Northern California. MARINe Annual Workshop, San Francisco, CA.

*Dalkey, A. and B. Allen. 2008. Palos Verdes Peninsula: research and education opportunities. MARINe Annual Workshop, San Pedro, CA.

*Douros, W. 2007. MARINe, marine sanctuaries and more. MARINe Annual Workshop, San Francisco, CA.

*Eernisse, D. 2008. Common chitons and limpets of southern California rocky intertidal. MARINe Annual Workshop, San Pedro, CA.

Elsberry, L.A. and J.L. Burnaford. 2010. The effects of low-tide exposure on the high intertidal alga *Endocladia muricata* in two geographic regions. Poster at Western Society of Naturalists Annual Meeting, San Diego, CA.

*Engle, J. 2007. Multi-Agency Rocky Intertidal Network status. MARINe Annual Workshop, San Francisco, CA.

*Engle, J. 2007. The Light and Smith Manual: invertebrate name changes. MARINe Annual Workshop, San Francisco, CA.

*Engle, J. 2008. MARINe aids NOAA Mussel Watch expansion in southern California. MARINe Annual Workshop, San Pedro, CA.

*Engle, J. 2008. Multi-Agency Rocky Intertidal Network status. MARINe Annual Workshop, San Pedro, CA.

*Engle, J. 2009. Multi-Agency Rocky Intertidal Network status. MARINe Annual Workshop, San Francisco, CA.

Fenberg, P.B. and K. Roy. 2007. The ecological consequences of size-selective harvesting: the owl limpet (*Lottia gigantea*) as a case study. Western Society of Naturalists Annual Meeting, Ventura, CA.

Flectcher, N.C., P.T. Raimondi, C.M. DaCosta, M.A. Redfield, and S.E. Worden. 2010. Poster at Western Society of Naturalists Annual Meeting, San Diego, CA.

*Fong, D. 2009. MARINe sites on Alcatraz. MARINe Annual Workshop, San Francisco, CA.

*Gaddam, R. 2008. Biodiversity surveys and PISCO updates. MARINe Annual Workshop, San Pedro, CA.

*Gaddam, R. 2009. Accessing MARINe data through the online PISCO data catalog. MARINe Annual Workshop, San Francisco, CA.

Garza, M.M. 2010. Relationship between habitat complexity and ochre sea star (*Pisaster ochraceus*) abundance. Poster at Western Society of Naturalists Annual Meeting, San Diego, CA.

*George, Maya, Christy Bell, Karah Ammann and Peter Raimondi. 2009. Assessing the amount of suitable habitat and the population size of black abalone from Half Moon Bay to Point Conception. Poster at Monterey National Marine Sanctuary Symposium, Monterey, CA.

*Gilbane, L. and J. Smith. 2008. MARINe training video. MARINe Annual Workshop, San Pedro, CA.

*Gilbane, L. and S. Kimura. 2009. Mapping: quest for the perfect map. MARINe Annual Workshop, San Francisco, CA.

*Gray, H. 2008. Common shorebirds of southern California rocky shores. MARINe Annual Workshop, San Pedro, CA.

*Gregorio, D. 2007. Areas of Special Biological Significance and MARINe. MARINe Annual Workshop, San Francisco, CA.

*Gregorio, D. and K. Schiff. 2008. California Areas of Special Biological Significance. MARINe Annual Workshop, San Pedro, CA.

Hays, CG. 2008. Genetic and maternal variation across a species' distribution: consequences for emersion tolerance in an intertidal alga. Seminars at California State University Sacramento; Sacramento, CA; and California State University San Jose; San Jose, CA.

Hays, CG. 2010. Genetic and maternal variation across a species' distribution: consequences for emersion tolerance in an intertidal alga. Seminar at Moss Landing Marine Lab, Moss Landing, CA.

*Helix, M.E. 2007. Overview of Multi-Agency Rocky Intertidal Network. MARINe Annual Workshop, San Francisco, CA.

*Helix, M.E. 2007. Rocky Intertidal Monitoring Network and the Southern California Coastal Ocean Observing System. SCCOOS Board of Governors Meeting June 13, 2007.

*Helix, M.E. 2008. Overview of Multi-Agency Rocky Intertidal Network. MARINe Annual Workshop, San Pedro, CA.

*Helix, M.E. 2009. Overview of Multi-Agency Rocky Intertidal Network. MARINe Annual Workshop, San Francisco, CA.

*Helix, M.E. 2010. Long-term monitoring program challenges – MARINe, the Multi-Agency Rocky Intertidal Network. Southern California Academy of Sciences Annual Meeting, Los Angeles, CA.

*Helix, M.E., P. Raimondi, R. Ambrose, J. Engle, and S. Murray. 2007. MARINe: examining the health of rocky shores along the Pacific Coast. Monterey Bay National Marine Sanctuary Currents Symposium, Monterey, CA.

*Helix, M.E., R.F. Ambrose, J.M. Engle, S.N. Murray, and P.T. Raimondi. 2007. Examining the health of rocky shores along the Pacific Coast – can local government and citizen's help? Coastal Zone 2007, Portland, OR.

Hewson, W.E. and D.J. Eernisse. 2007. A common southern California limpet is a new species that overlaps with its sister species in northern Baja California. Western Society of Naturalists Annual Meeting, Ventura, CA.

*Joab, B. and J. Cubit. 2008. MARINe and NRDA's: increasing the effectiveness of the combination. MARINe Annual Workshop, San Pedro, CA.

*Jones, A.M. and D.P. Lohse. 2009. A regional comparison of *Mytilus californianus* growth rates along the central coast of California. Western Society of Naturalists Annual Meeting, Monterey, CA.

*Kimura, S. 2007. GIS maps of the California coastline. MARINe Annual Workshop, San Francisco, CA.

*Kinyon, J. 2009. Habitat mapping in Golden Gate National Recreation Area. MARINe Annual Workshop, San Francisco, CA.

*Lawrenz-Miller, S. 2008. Long term intertidal population surveys on the Palos Verdes Peninsula. MARINe Annual Workshop, San Pedro, CA.

*Lee, S. 2008. MARINe site at Point Fermin. MARINe Annual Workshop, San Pedro, CA.

*Lee, S. 2008. Multi-Agency Rocky Intertidal Network. Teacher Training Workshop for Center for Ocean Sciences Education Excellence (COSEE-West), San Pedro, CA.

*Lee, S. 2009. Survey team monitoring summary: LA/Ventura Counties. MARINe Annual Workshop, San Francisco, CA.

*Livingston, H. 2009. Species ranges: climate change implications. MARINe Annual Workshop, San Francisco, CA.

*Long, J. 2007. MARINe on the East Coast. MARINe Annual Workshop, San Francisco, CA.

*Long, J. 2008. MARINe on the East Coast. MARINe Annual Workshop, San Pedro, CA.

*Long, J. 2009. Survey team monitoring summary: East Coast. MARINe Annual Workshop, San Francisco, CA.

*Lonhart, S. 2007. MARINe regional sampling update: Central California. MARINe Annual Workshop, San Francisco, CA.

*Maloney, E. 2008. California Introduced Species Surveys: who's on our turf? MARINe Annual Workshop, San Pedro, CA.

Maloney, E.R., W.R. Fairey, A.A. Lyman, Z.A. Walton, S.F. Foss, and S.N. Shiba. 2008. Surveys for introduced marine species on the outer coast of California: who's on our turf? Western Society of Naturalists Annual Meeting, Vancouver, BC.

*Miller, K.A. 2009. Invasive species status. MARINe Annual Workshop, San Francisco, CA.

Miller, K.A. 2010. California's non-native seaweeds: a case study. XX International Seaweed Symposium, Ensenada, Baja California, Mexico.

*Miner, C.M. 2008. MARINe database structure. MARINe Meeting, Seattle, WA

*Miner, C.M. 2008. MARINe Rocky Intertidal Monitoring Program, Northwest Straits Initiative Meeting, Bellingham, WA

*Miner, M. 2007. Multi-Agency Rocky Intertidal Network database update. MARINe Annual Workshop, San Francisco, CA.

*Miner, M. 2008. Multi-Agency Rocky Intertidal Network database update. MARINe Annual Workshop, San Pedro, CA.

*Miner, M. 2009. Survey team monitoring summary: Washington State. MARINe Annual Workshop, San Francisco, CA.

Monaco, C.J. 2010. Size-dependent intertidal distribution and foraging behavior in *Pisaster ochraceus*. Poster at Western Society of Naturalists Annual Meeting, San Diego, CA.

*Murray, S. 2007. Science, politics, the public and protecting California's coastal ecosystems. Southern California Academy of Sciences Annual Meeting, Fullerton, CA.

*Murray, S. 2008. Changes in rocky intertidal communities on the Channel Islands and the southern California mainland since the 1970's. 7th California Islands Symposium, Oxnard, CA.

*Murray, S., R.F. Ambrose, J. Engle, P. Raimondi, and S. Weisberg. 2010. Developing indicators for monitoring the status of rocky shores. California and the World Ocean 2010 Conference, San Francisco, CA.

*Murray, S.N., C.A. Navarro, S.C. Vogt, and J.R. Smith. 2010. Feeding responses of native macro-invertebrates to non-indigenous seaweeds. XX International Seaweed Symposium, Ensenada, Baja California, Mexico.

*Murray, S.N., J. R. Smith, A. Bullard, and L. Gilbane. 2009. Changes in Coastal Seaweed Populations over time in Urban Settings and the Ecological Implications (Plenary Lecture). Novos Bioativos de Macroalgas Workshop, Ilhabela – São Paulo, Brazil.

*Murray. S. N. 2008. Seaweed Introductions: An Overview. Control of Invasive Marine Seaweeds Workshop, Asilomar, CA.

*Navarro, C. 2007. MARINe regional sampling update: Southern California. MARINe Annual Workshop, San Francisco, CA.

*Navarro, C.N., J.R. Smith, and S.N. Murray. 2007. Feeding rates of native consumers on introduced and native seaweeds on urban southern California shores. Southern California Academy of Sciences Annual Meeting, Fullerton, CA.

*Neuman, M.J. and G.R. VanBlaricom. 2008. Status of black abalone populations at the California Channel Islands: implications for long-term viability throughout the range of the species. 7th California Islands Symposium, Oxnard, CA.

Orr, D., P. Raimondi, C. Bell, T. Conway-Cranos, M. George, D. Lohse, and S. Worden. 2010. Assessment of effect and predictions of recovery dynamics when baseline data are scarce: a case study of the Cosco Busan oil spill. Western Society of Naturalists Annual Meeting, San Diego, CA.

*Orr, D.W., M.A. Redfield, L.M. Anderson, K.N. Ammann. 2010. Overview of the biological sampling used to assess California's Central Coast Marine Protected Areas – with an emphasis on rocky intertidal habitats. Poster at Monterey Bay National Marine Sanctuary Symposium, Monterey, CA.

Parker, M.A. and K.J. Nielsen. 2007. A tale of two headlands: recruitment and reproductive output of *Balanus glandula* and *Chthamalus dalli* along the northern California coast. Western Society of Naturalists Annual Meeting, Ventura, CA.

Pearse, J.S., D.E. Pearse, and V.B. Pearse. 2007. Rising sea level and changes in intertidal zonation: professor Snadrock 60 years later. Western Society of Naturalists Annual Meeting, Ventura, CA.

Pister, B. and T. Philippi. 2010. Twenty years of rocky intertidal monitoring at Cabrillo National Monument: detection and analysis of long-term trends. Western Society of Naturalists Annual Meeting, San Diego, CA.

*Protopapadakis, L. 2008. California's Marine Life Protection Act: laying a foundation for the future. MARINe Annual Workshop, San Pedro, CA.

*Raimondi, P. 2007. MARINe and Marine Protected Areas. MARINe Annual Workshop, San Francisco, CA.

*Raimondi, P., D. Gregorio, and A. Compton. 2007. Rocky intertidal health. MARINe Annual Workshop, San Francisco, CA.

*Raimondi, P.T. 2008. Go-kit protocols updated through Cosco Busan Experience. MARINe Annual Workshop, San Pedro, CA.

Recchia, C., L. Whitman, P. Raimondi, A. Scholz, S. Murray, and S. Katz. 2010. Evolving MPA monitoring: aligning science and policy. California and the World Ocean 2010 Conference, San Francisco, CA.

*Redfield, M. 2009. Survey team monitoring summary: Monterey/Marin Counties. MARINe Annual Workshop, San Francisco, CA.

Redfield, M.A., P.T. Raimondi, N.C. Fletcher, and S.E. Worden. 2010. An overview of the North Central Coast Marine Protected Areas Baseline Program monitoring. Poster at Western Society of Naturalists Annual Meeting, San Diego, CA.

Reinhard, L.J., K.N. Ammann, M.T. Tinker, P.T. Raimondi, and C.A. Bell. 2009. Effects of sea otters on local distribution and density of black abalone. Western Society of Naturalists Annual Meeting, Monterey, CA.

Richards, D. 2008. Foundations of Marine Reserves at the Channel Islands, NPS Aquatic Professionals Meeting, Fort Collins, CO.

*Richards, D. 2009. Black abalone restoration/recovery plan status. MARINe Annual Workshop, San Francisco, CA.

Richards, D. 2009. Marine Reserves at the Channel Islands. George Wright Society Meeting, Portland, OR.

*Richards, D. 2009. Survey team monitoring summary: Channel Islands. MARINe Annual Workshop, San Francisco, CA.

Richards, D.V. 2008. Black abalone at the Channel Islands, a brief history. 7th California Islands Symposium, Oxnard, CA.

Richards, D.V. and S.G. Whitaker. 2010. Monitoring black abalone movement and aggregating behavior. Poster at Western Society of Naturalists Annual Meeting, San Diego, CA.

Sagarin, R.D. 2008. Size matters: loss of large coastal invertebrates and implications for ecology and management. Western Society of Naturalists Annual Meeting, Vancouver, BC.

*Smith, J.R. 2007. Long-term change in macrophyte & macroinvertebrate communities on wave-exposed rocky intertidal shores. Seminar at California State University, Northridge, Department of Biology, Biology Colloquium.

*Smith, J.R. 2007. Seaweed communities in a heavily urbanized environment in southern California. Seminar at the Coastal Studies Consortium, Universidade Federal Fluminense, Niteroi, Brazil.

*Smith, J.R. 2008. Coastal ecology in the face urbanization and environmental change. Seminars at Eastern Connecticut State University, and NOAA Workshop on Managing Visitor Use at Dana Point, CA.

*Smith, J.R. 2009. Coastal urban ecology for teachers. Seminar for Centers for Ocean Sciences Education Excellence (COSEE) at Dana Point, CA.

*Smith, J.R. 2009. Survey team monitoring summary: San Diego/Orange Counties. MARINe Annual Workshop, San Francisco, CA.

*Smith, J.R. 2009. Urban ecology: a southern California rocky intertidal perspective. Seminars at SUNY Stony Brook Southampton, NY, CA State University Fullerton, and University of Alaska Southeast.

*Smith, J.R. 2010. Urban ecology: a southern California rocky intertidal perspective. Seminars at California Polytechnic University, CA and University of New Haven, CT.

*Smith, J.R., R.F. Ambrose, and P. Fong. 2008. Regional comparisons and decadal changes in mussel populations (*Mytilus californianus*) and mussel bed community diversity along the California coast. 7th California Islands Symposium, Oxnard, CA.

*Smith, J.R., S.G. Whitaker, and S.N. Murray. 2009. Experimental re-establishment of the rockweed, *Silvetia compressa*, on urban southern California shores. Western Society of Naturalists Annual Meeting, Monterey, CA.

Smith, K.A. and B. Helmuth. 2007. When mussels die…an assessment of the mechanisms determining the upper limit of Mytilus californianus beds along the Pacific coast of North America. Western Society of Naturalists Annual Meeting, Ventura, CA.

Steinbeck, J.R. 2010. Sh%t happens: how designing redundancy into a monitoring program can help exorcise intruding demons and increase the options for analysis and ability to detect change. . Southern California Academy of Sciences Annual Meeting, Los Angeles, CA.

SWAT. 2008. Life in the tidepools and kelp forests. Seminar at Rancho del Oso Nature Center.

*Tharratt, S. 2007. MARINe regional sampling update: offshore islands. MARINe Annual Workshop, San Francisco, CA.

Thompson, S.A., K.J. Nielsen, C.A. Blanchette, B. Brockbank, and H.R. Knoll. 2007. Effects of commercial collection on growth and reproductive output of *Postelsia palmaeformis*. Ecological Society of America Annual Meeting, San Jose, CA.

Thompson, S.A., K.J. Nielsen, C.A. Blanchette, B. Brockbank, and H.R. Knoll. 2007. The response of *Postelsia palmaeformis* to commercial collection across sites in California. Western Society of Naturalists, Ventura, CA.

*Vogt, S., J.R. Smith, and S.N. Murray. 2010. Do native macro-invertebrates consume native over non-native seaweeds? Northwest Algal Symposium, Whidbey Island, WA.

*Vogt, S.C., J.R. Smith, and S.N. Murray. 2010. The consumer's dilemma, native or non-native seaweeds. Western Society of Naturalists Annual Meeting, San Diego, CA.

*Vogt, S.C., L. Gilbane, A. Bullard, J.R. Smith, and S.N. Murray. 2007. Spatial and temporal variation in $\delta^{13}C$ and $\delta^{15}N$ values of macro-algae in southern California waters. Southern California Academy of Sciences Annual Meeting, Fullerton, CA.

*Walters, K. 2009. Survey team monitoring summary: Mexico/Baja California. MARINe Annual Workshop, San Francisco, CA.

*Walters, K. 2009. Today's GPS: what it can do for you – a SWAT retrospective. MARINe Annual Workshop, San Francisco, CA.

Waltz, G.T., J.R. Steinbeck, S.R. Kimura, and D.E. Wendt. 2007. Simulation of human activities and corresponding impacts to the temperate intertidal. Western Society of Naturalists, Ventura, CA.

Waltz, G.T., S. Kimura, J.R. Steinbeck, and D.E. Wendt. 2009. Bare space or bountiful biota: an analysis of human disturbance on our rocky shoreline. Western Society of Naturalists Annual Meeting, Monterey, CA.

*Weisberg, S.B. 2008. The subtle benefits of cooperative regional monitoring. MARINe Annual Workshop, San Pedro, CA.

Whitaker, S. 2008. Experimental re-establishment of the rockweed Silvetia compressa at Little Corona del Mar. MARINe Annual Workshop, San Pedro, CA.

Whitaker, S.G. and D.V. Richards. 2010. Widespread declines in abundances of rocky intertidal ecosystem modifiers and associated motile invertebrate species. Poster at Western Society of Naturalists Annual Meeting, San Diego, CA.

*Whitaker, S.G., J.R. Smith, and S.N. Murray. 2007. Experimental restoration of the rocky intertidal brown alga *Silvetia compressa* on urban southern California shores. Southern California Academy of Sciences Annual Meeting, Fullerton, CA.

*Whiteside, K.E., J.R. Smith, and S.N. Murray. 2007. Distribution, habitat utilization, and reproductive patterns in *Caulacanthus ustulatus* (Caulacanthaceae, Gigartinales), a newly established seaweed on southern California shores. Southern California Academy of Sciences Annual Meeting, Fullerton, CA.

*Worden, S. 2009. What is larval recruitment data telling us? MARINe Annual Workshop, San Francisco, CA.

Publications (2007-2010)

Ambrose, R.F. 2008. Habitat restoration. Pp. 260-263. In: M.W. Denny and S.D. Gaines (eds.). *Encyclopedia of Tidepools & Rocky Shores*. University of California Press, Berkeley, CA.

Becker, B.J., L.A. Levin, F.J. Fodrie, and P.A. McMillan. 2007. Complex larval connectivity patterns among marine invertebrate populations. *Proceedings of the National Academy of Sciences* 104:3267-3272.

Blanchette, C.A. and S.D. Gaines. 2007. Distribution, abundance, size and recruitment of the mussel, *Mytilus californianus*, across a major oceanographic and biogeographic boundary at Point Conception, California, USA. *Journal of Experimental Marine Biology and Ecology* 340:268-279.

Blanchette, C.A., B. Helmuth, and S.D. Gaines. 2007. Spatial patterns of growth in the mussel, *Mytilus californianus*, across a major oceanographic and biogeographic boundary at Point Conception, California, USA. *Journal of Experimental Marine Biology and Ecology* 340:126-148.

Blanchette, C.A., C.M. Miner, P.T. Raimondi, D. Lohse, K.E.K. Heady and B. Broitman. 2008. Biogeographic patterns of rocky intertidal communities along the Pacific coast of North America. *Journal of Biogeography* 35:1593-1607.

Blanchette, C.A., D.R. Schiel, E.A. Wieters, B.R. Broitman, and B.P. Kinlan. 2009. Trophic structure and diversity in rocky intertidal upwelling ecosystems: A comparison of community patterns across California, Chile, South Africa and New Zealand. *Progress in Oceanography* 83:107-116.

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Sample Data Requests (2010)

**CSU Monterey Bay – Clover Lee*
Project: GIS predictive habitat model for black abalone
Data Request: Black abalone habitat assessment data from 2007-2008

**UCSB – Stephen Gosnell*
Project: Modeling sea star density and distribution along the coast
Data Request: *Pisaster* and Whelk density data at MARINe sites

UCSB – Carola Flores Fernandez
Project: Integration of ecological, archaological, and paleoclimatic data in the study of past marine ecosystems
Data Request: Shellfish abundance and mussel growth data for Channel Islands sites

**Duke University – Cliff Cunningham*
Project: Barnacle mortality as it relates to predator abundance and temperature
Data Request: Site temperature data and Motile data, as well as general site information (bolt to bolts, maps, site summaries, tidal heights).

**MBNMS – Steve Lonhart*
Project: Determining areas where abalone may be present, for use in National Marine Sanctuary permitting process.
Data Request: Lat/Longs and black abalone presence information at intertidal study sites between Pt Arena and Government Pt.

**University of South Carolina – Cristian Monaco*
Project: Interaction between *Pisaster ochraceus* and *Mytilus californianus*
Data Request: All *Pisaster* and *Mytilus* density estimates, as well as *Pisaster* size data

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APPENDIX

Selected Publications (attached)

Henkel, S.K. and S.N. Murray. 2007. Reproduction and morphological variation in southern California populations of the lower intertidal kelp *Egregia menziezii* (Laminariales). Journal of Phycology 43:242-255

Murray, S.N., P. Raimondi, and S.B. Weisberg. 2010. In pursuit of bio-criteria for evaluating the condition of rocky intertidal communities. Report of a workshop sponsored by the University of Southern California Sea Grant Program. with assistance from the Bureau of Ocean Energy Management, Regulation and Enforcement. 11p.

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REPRODUCTION AND MORPHOLOGICAL VARIATION IN SOUTHERN CALIFORNIA POPULATIONS OF THE LOWER INTERTIDAL KELP *EGREGIA MENZIESII* (LAMINARIALES)[1]

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Intertidal *Egregia menziesii* (Turner) Aresch. populations were studied at three Southern California sites to determine temporal and spatial patterns of reproduction and morphology. The timing of sporophyll production and sporophyte recruitment was similar at all sites. Sporophyll production was much greater during winter periods of colder seawater temperatures and shorter day lengths. Sporophyte recruitment occurred from spring through midsummer, ~5 months following maximal sporophyll production. Lateral blade morphologies varied in a consistent manner, suggesting a developmental mechanism for form variation in *Egregia* thalli. Spatulate blades dominated shorter axes and the bases of longer axes, whereas filiform laterals became abundant toward the tips of longer axes. Filiform laterals ($9.8\,\mathrm{mg\,O_2 \cdot g^{-1} \cdot h^{-1}}$) had higher light-saturated net photosynthetic rates than spatulate laterals ($6.8\,\mathrm{mg\,O_2 \cdot g^{-1} \cdot h^{-1}}$), resulting in a 12% increase in the productivity of *Egregia* per meter of filiform frond.

Key index words: ***Egregia*; herbivory; intertidal; kelp; morphology; photosynthesis; reproduction**

Kelps are conspicuous components of temperate seaweed communities in the eastern North Pacific (North 1971, Foster and Schiel 1985), and these large brown algae often exhibit species-specific variations in reproductive strategies (Reed et al. 1996) and morphology (North 1971, Hurd 2000) in relation to environmental factors. Morphological variation, however, has been closely examined for few kelps, probably because of their large size and relative ease of identification. Previous research on internal and external thallus morphology has focused mostly on the effects of wave exposure (Parke 1948, Sundene 1962a, b, 1964, Chapman 1973, Palmisano and Sheng 1977, Gerard and Mann 1979, Gerard 1987, Roberson 2001) and the effect on turbulence (Koehl and Alberte 1988, Hurd and Stevens 1997, Hurd et al. 1997), mass transfer (Koehl and Alberte 1988, Hurd et al. 1996), and photon capture (Koehl and Alberte 1988, Wing and Patterson 1993, Wing et al. 1993).

Egregia menziesii is one of the most variable and complex of the kelps (Setchell 1893, Fritsch 1945), with an adult morphology distinct from other species. Thallus fronds can reach up to 15 m in length and consist of basal stipes that flatten to rachi as they become lined with lateral blades and sporophylls (Setchell 1893, Setchell and Gardner 1925, Abbott and Hollenberg 1976). *Egregia* is distributed from Alaska to Punta Eugenio, Baja California, México, and grows intertidally to depths of at least 20 m (Abbott and Hollenberg 1976). The life history of *Egregia* is typical of members of the order Laminariales, consisting of a microscopic gametophyte and a conspicuous, perennial sporophyte. Zoospores produced in morphologically distinct sporophylls (Setchell 1893, Setchell and Gardner 1925, Yoon et al. 2001) settle and germinate into gametophytes, which in turn produce eggs and sperm that upon fertilization give rise to embryonic sporophytes (Myers 1928). Fertility of *Egregia* occurs from spring to fall in British Columbia (Gordon and De Wreede 1978) and presumably central California (Abbott and Hollenberg 1976); sporophyte recruitment in Southern California has been observed from January to June (Black 1974, Murray and Littler 1977, Gunnill 1980, 1985).

Egregia morphology varies considerably throughout its range and is believed to correlate with geographic distribution (Abbott and Hollenberg 1976, Blanchette et al. 2002). Historically, at least two and as many as five species and subspecies of *Egregia* were recognized based largely on variations in the morphology of the rachis and lateral blades (Setchell and Gardner 1925, Silva 1957, Chapman 1962a). However, despite this high degree of morphological variation, currently only one species (*E. menziesii*) and no subspecies of *Egregia* are recognized (Abbott and Hollenberg 1976).

The lateral blades of *Egregia* can range from broad, ovate, or spatulate to highly dissected and filiform and

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vary not only among thalli separated by many kilometers but also within local populations growing on the same or nearby shores (Chapman 1962a). Besides representing possible ecotypic variation, differences in lateral morphology may have ecological implications (Littler 1980, Littler and Littler 1980). For example, variations in lateral morphology may result in differences in thallus productivity (Odum et al. 1958, Chapman 1962b, Littler and Arnold 1982) and resistance to herbivory (Littler and Littler 1980; but see Padilla and Allen 2000).

The purpose of this study was to determine the timing of reproduction and recruitment and to examine variations in thallus and lateral blade morphology in *Egregia* populations at three Southern California sites. Prior studies indicate that gametophyte fertility is reduced or inhibited at temperatures exceeding 16°C (Myers 1928, Lüning and Neushul 1978). Thus, we hypothesized that our Southern California populations of *Egregia* would produce fertile sporophylls mostly during fall and winter. Because the appearance of young *Egregia* thalli has been observed from late spring to early summer (Black 1974, Murray and Littler 1977, Gunnill 1980, 1985), we hypothesized that peak recruitment of juvenile sporophytes would be related to the fall and winter periods of sporophyll production. Morphological plasticity is widespread among seaweeds and often reflects environmental conditions (Dixon 1970, Hay 1981, Mathieson et al. 1981, Lewis et al. 1987, Kilar and Hanisak 1989). Thus, we also hypothesized that *Egregia* morphology would vary with differences in site conditions, such as wave exposure or herbivory, and based on prior research (Chapman 1962b, Littler and Littler 1980, Littler and Arnold 1982), we predicted that variations in *Egregia* lateral morphology would result in differences in thallus productivity.

METHODS AND MATERIALS

Site descriptions. This research was conducted at three Southern California sites: Crystal Cove (33°34.3′ N, 117°50.3′ W), Shaw's Cove (33°32.8′ N, 117°48.2′ W), and Dana Point (33°27′ N, 117°43′ W), selected for their high intertidal standing stocks of *Egregia* at the initiation of the study (Fig. 1). These sites were distributed along an ∼15.5 km section of southwest facing coastline, which experiences moderate wave exposure due to protection by the Channel Islands (Ricketts et al. 1985, Hickey 1993). The average maximum wave force was greatest at Dana Point ($5.15 \pm 0.27\,\mathrm{m \cdot s^{-1}}$) followed by Crystal Cove ($4.89 \pm 0.08\,\mathrm{m \cdot s^{-1}}$) and Shaw's Cove ($4.86 \pm 0.17\,\mathrm{m \cdot s^{-1}}$) based on data obtained in midshore rockweed habitats during fall and winter of 1997 (Sapper and Murray 2003). Measurements taken throughout the year indicate that the three sites exhibit little site-to-site variation in daily sea temperature (≤ 1°C) and salinity (≤ 1‰). However, annual sea temperatures in the region vary greatly by season and ranged from 10°C to 22°C during the study (unpublished data from Balboa reference station; Marine Life Research Group, Scripps Institution of Oceanography, La Jolla, CA).

The three study sites varied in substratum topography and herbivore pressure. At Crystal Cove, flattened and angled benches were separated by shallow channels located between uplifted bedding planes. The study area was frequently inundated with sand, which at times covered *Egregia* holdfasts and portions of stipes. The Shaw's Cove sampling area was located in a surge channel; here, *Egregia* was observed growing on large, stable boulders and on channel sides below mussel beds. Granitic boulders mixed with flattened benches characterized the Dana Point study site. Qualitative observations indicated that grazing on *Egregia* was greatest at Shaw's Cove where high densities of purple sea urchins [*Strongylocentrotus purpuratus* (Stimpson)] and kelp snails [*Norrisia norrisi* (Sowerby)] were concentrated in the surge channel, where they were observed feeding on *Egregia*. *Strongylocentrotus purpuratus* and occasionally the red sea urchin *S. franciscanus* (Agassiz) and *N. norrisi* were present but not abundant at Dana Point. Sea urchins were not encountered in the immediate Crystal Cove study area, and kelp snails were rare.

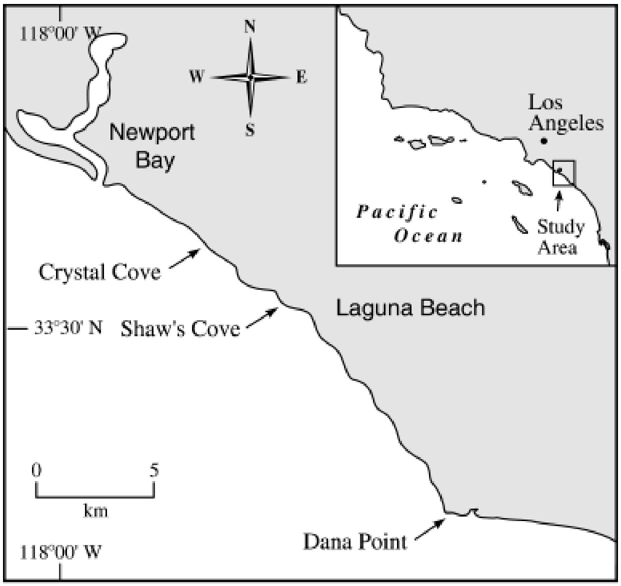

FIG. 1. Location of the three Southern California study sites: Crystal Cove, Shaw's Cove, and Dana Point.

Recruitment and population structure. Recruitment of young *Egregia* sporophytes at each of the three sites was determined quarterly from January 2001 to February 2002. Results from sampling performed during 2001 supported the prediction that *Egregia* sporophyte recruitment would occur during spring; consequently, in 2002, each site was sampled monthly from March to July to more precisely determine the magnitude and timing of sporophyte recruitment. Permanent transect lines (10–12 m in length) were placed parallel to the shore through *Egregia* populations at about Mean Lower Low Water. At Crystal Cove and Dana Point, three bands were established perpendicular to transects during each site visit using a random-number table. However, at Shaw's Cove, the three bands were fixed and located where thalli were most dense at the initiation of the study due to high topographical heterogeneity and the patchy distribution of *Egregia* in the surge channel. Each band was 1 m wide and 6 m long, resulting in six contiguous 1 m×1 m plots that extended 3 m above and 3 m below the horizontal transect. Within each plot, the number of *Egregia* sporophytes was recorded and all *Egregia* thalli were assigned to one of four (Types I–IV) developmental stages (Fig. 2). A Type I recruit was defined as a laminarialean juvenile with a single, short blade. With the exception of only the smallest juvenile sporophytes (<4 cm in length), Type I *Egregia* recruits could be distinguished from *Eisenia arborea* Aresch. recruits because

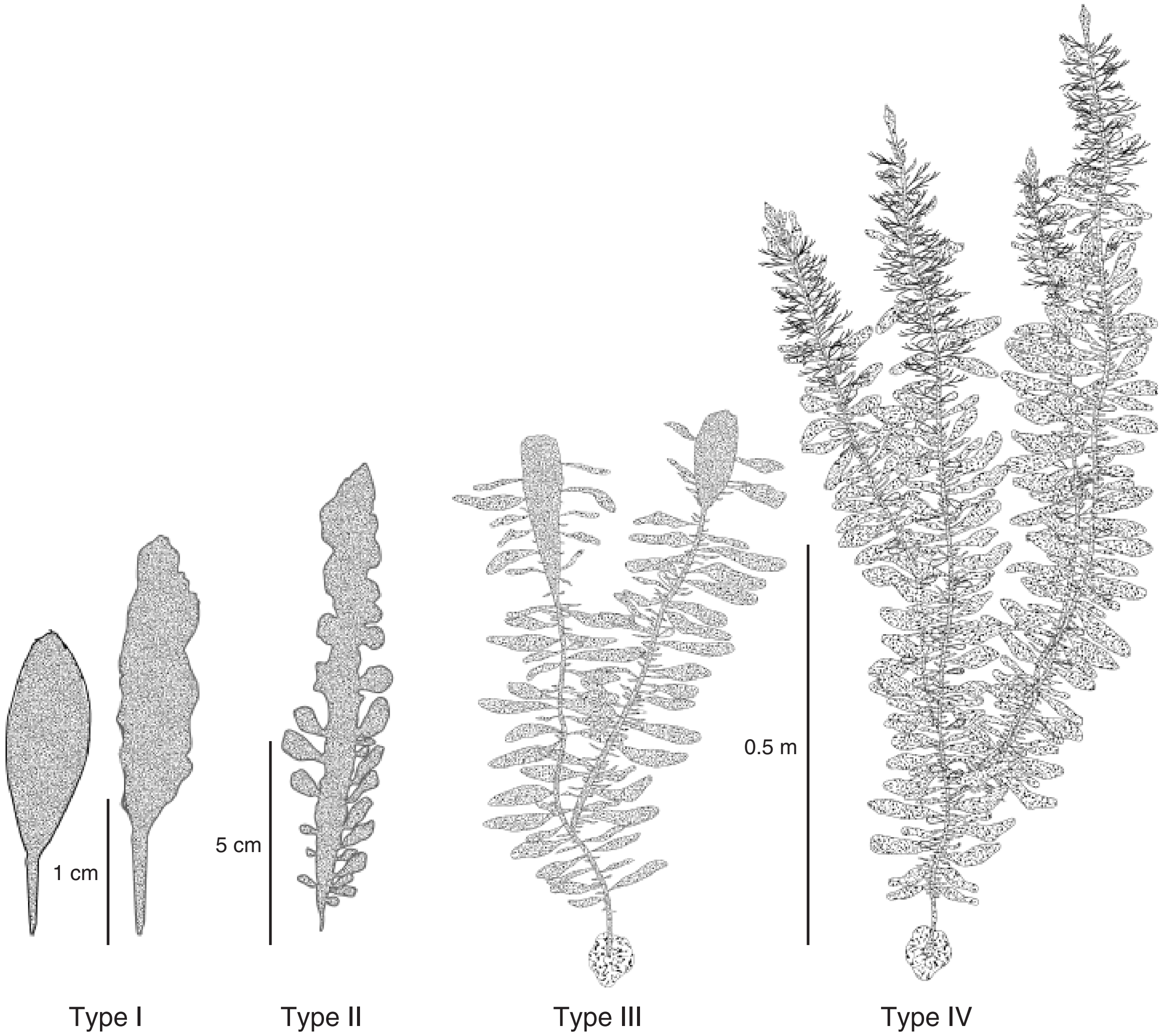

FIG. 2. Developmental stages of *Egregia* sporophytes. Type I: short stipe and single blade. Type II: single blade with marginal leaflets. Type III: short branching thallus with well-developed rachi (<25 cm), <3 pneumatocysts, and terminal blades deteriorating. Type IV: Differentiated, mature sporophyte. Scale bar, 0.5 m for stages III and IV.

Egregia juveniles had smooth blades, whereas *E. arborea* juveniles had wrinkled or corrugated blades. No other kelps were observed to recruit into intertidal habitats at our sites during the study. Type II *Egregia* juveniles had a single blade with marginal leaflets. Type III (subadult) was defined as a short (≤25 cm) branching thallus with a well-developed rachis and less than three pneumatocysts. Type IV was a mature, differentiated *Egregia* thallus possessing more than one axis and more than three pneumatocysts.

Morphological features of mature *Egregia* thalli were determined at the three sites. The nearest Type IV *Egregia* thallus within a 0.5 m radius of each 1.0 m mark along each transect was identified to generate a sample size of 12–22 individuals per site visit. The longest axis of each thallus was measured from holdfast to tip, and the total number of axes was counted. The numbers of viable (with meristem) and nonviable (*sans* meristem) axes also were determined.

Sporophyll production and lateral morphologies. Patterns of *Egregia* sporophyll production and lateral blade morphology at each site were determined monthly from February 2001 to February 2002. Nine thalli growing adjacent to sampled populations were haphazardly selected, and the first axis of each thallus with an intact meristem and a length >50 cm was excised and taken to the laboratory. Each axis was divided into five 5 cm sections such that 5 cm located just below the meristem was sampled, 5 cm just above the base of the axis was sampled, and the three remaining 5 cm sections were evenly dispersed between the apical and basal sections. Vegetative lateral blades and sporophylls were counted in each section. Vegetative laterals were assigned to one of three morphs (filiform, spatulate, or intermediate; Fig. 3) to characterize patterns of lateral morphology; the percentage of each morph was determined relative to axis location for each sampled thallus.

Reproductive periodicity was determined by the density of sporophylls along the same axis sections. To ensure that the sporophylls counted were fertile, one axis from each site was randomly selected each month that axes with sporophylls were collected. Five sporophylls were then haphazardly excised and sectioned to check microscopically for the presence of mature sporangia. The amount of biomass allocated to sporophyll production was also estimated for each *Egregia* axis. Subsamples of

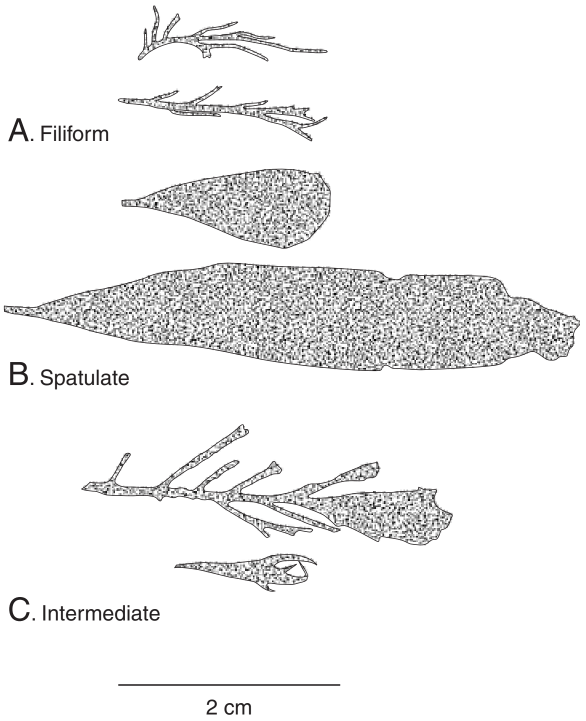

FIG. 3. Vegetative lateral types used in morphological analyses of *Egregia* axes.

sporophylls, each lateral morph, and sections of the rachis were dried to constant weight at 60°C. The percentage of *Egregia* biomass allocated to sporophylls was determined using the mean dry weights (dwt) of these subsamples and their abundances, and the dwt to length relationship for the rachis.

Herbivore densities. The primary benthic herbivores observed feeding on *Egregia* at the three sites included *Strongylocentrotus* spp. (urchins); *N. norrisi* (kelp snail); and *Notoacmaea insessa* (Hinds), a limpet that lives and feeds on the *Egregia* rachis (Black 1976). In order to quantify differences in herbivore abundances, and presumably grazing pressure, among the three sites, the numbers of red and purple urchins and kelp snails in each plot were determined, and the number of *N. insessa* on each measured Type IV *Egregia* thallus was recorded.

Photosynthesis experiments. Photosynthetic rates of different parts of *Egregia* thalli were determined in the field at Dana Point, California, on March 11, and April 4 and 16, 2002, following methods similar to those described by Littler and Arnold (1980, 1985). Spatulate blades, filiform laterals, intermediate laterals, sporophylls, and bare rachi without epiphytes were excised from freshly collected *Egregia* thalli and submerged in trays for 1–2 h before incubation. Four to six replicates of each thallus part were then incubated in filtered (10 μm) seawater for 1±0.5 h (light treatments) or 2±0.5 h (dark treatments) within closed 0.5 L French square glass bottles. During incubations, bottles were kept submerged in shallow plastic trays, which were replenished with seawater every 10–15 min to maintain ambient seawater temperature. Incubation bottles were thoroughly mixed every 5–10 min using magnetic stirrers to break down diffusion barriers. Changes in dissolved oxygen (DO) concentration were measured with Yellow Springs Instruments™ oxygen electrodes (Yellow Springs, OH, USA) and used to calculate net photosynthetic and dark respiration rates. Following incubations, thallus parts were returned to the laboratory and dried to constant weight at 60°C. Light (318–974 μmol photons · m^{-2} · s^{-1}) and temperature (15–19°C) varied among experiments; however, analyses failed to show statistically significant differences in net photosynthetic and dark respiration rates among experiments performed on different days and under the range of temperature and light conditions employed. Hence, data from all sampling dates were pooled for analysis. Photosynthetic rates are believed to represent light-saturated values based on reports of requirements for saturating intertidal seaweeds (300–1200 μmol photons · m^{-2} · s^{-1}; Lüning 1981).

Statistical analyses. Each data set was examined for variance homogeneity using Cochran's and Levene's tests and transformed if necessary to meet parametric requirements. A one-way analysis of variance (ANOVA) was used to test the hypothesis that photosynthetic and dark respiration rates differed among thallus parts. Where differences were significant, Student–Newman–Keuls' multiple comparison tests were used to differentiate subsets of means to facilitate interpretation of ANOVA results. Two-way ANOVA models were employed to analyze the effects of the fixed factors site and sampling period on the numbers of sporophylls, numbers of different lateral morphs, maximum axis length, and the percentage of viable axes. Variance criteria were met either by the original data or following transformation in all analyses.

The nonparametric Spearman's rank correlation procedure was used to determine whether a statistical relationship could be detected between seasonal patterns of sporophyll production and seawater temperatures or photoperiods. Surface seawater temperatures (SSTs) used in this analysis were obtained from the Balboa, Newport Beach, CA, reference station (Marine Life Research Group, Scripps Institution of Oceanography; unpublished data), whereas hours of daylight were calculated from sunrise and sunset data reported in National Oceanographic and Atmospheric Association (NOAA) tide tables for outer Newport Bay (Anonymous 1998).

RESULTS

Sporophyll production. The morphology of *Egregia* sporophylls varied depending on the form of the associated vegetative laterals. Sporophylls associated with filiform laterals were thick, strongly furrowed, and raisin-like in appearance, with filiform extensions often seen growing from sporophyll termini. In contrast, sporophylls produced in spatulate regions of the axis were flattened, with plump and wrinkled basal portions (Fig. 4). Microscopic examination revealed that almost all examined sporophylls had fertile sori and that fertile sori could be detected year-round (Table 1). The greatest proportion of examined sporophylls were fertile during winter. Sporophylls with mature sporangia tended to be darker and more wrinkled but were of similar thickness as nonfertile sporophylls.

Sporophyll production varied greatly over time ($F_{11,286} = 16.593$, $P<0.001$) but did not vary among sites ($F_{2,286} = 2.475$, $P = 0.08$; two-way ANOVA); a significant interaction between time and sites was not detected ($F_{22,286} = 1.528$, $P = 0.06$), suggesting that the seasonal patterns of sporophyll production were similar at the three sites (Fig. 5). Sporophyll

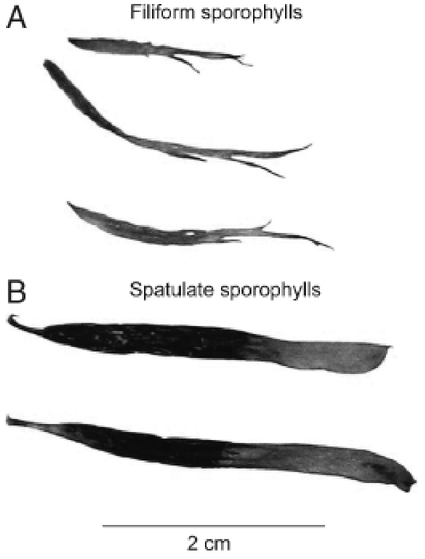

FIG. 4. Variable sporophyll morphologies. (A) Filiform sporophylls. (B) Spatulate sporophylls.

production was much greater in December and January, during periods of colder mean monthly ocean temperatures (11–13°C) and shortest daylight hours (9.9–10.5 h), and least during the periods of warmer sea temperatures (17–19°C) and longer days (12.5–14.5 h). Sporophyll densities exhibited significant negative correlations with both sea temperature ($r = -0.50$; $P = 0.02$) and hours of daylight ($r = -0.81$; $P < 0.001$). At all sites, densities of *Egregia* sporophylls were high (3.1–3.8 $\text{cm} \cdot \text{axis}^{-1}$) at the initiation of the study in winter 2001 and then dropped to nearly zero by spring. The number of sporophylls varied greatly among thalli but remained low for most of the summer before peaking again (5.0–7.9 $\text{cm} \cdot \text{axis}^{-1}$) the next winter between November and January. Although variable among sites, small, short-lived increases in summer sporophyll production appeared to follow periods when ocean temperatures at the Balboa reference station dropped for a few days to 13°C. The amount of total biomass (above the holdfast) allocated to sporophyll production showed a seasonal pattern similar to sporophyll densities. The percentage of dry biomass allocated to reproductive tissues, pooled across sites, ranged from a low of 0.6% in July 2001 to a high of 14.9% in January 2002, the period of greatest sporophyll production (Fig. 5).

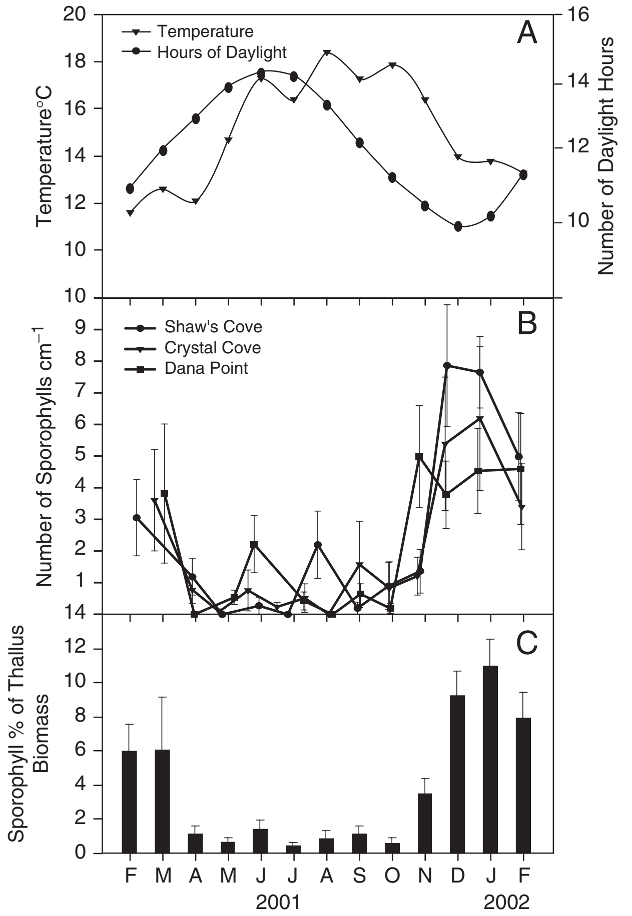

FIG. 5. (A) Surface seawater temperatures and hours of daylight during the study period (monthly means). (B) Patterns of sporophyll production in *Egregia menziesii* populations from the three study sites. Values are monthly means (±1 SE) of sporophyll numbers per cm of axis for nine replicates from each site. (C) Mean (+1 SE) percentage of dry biomass allocated to sporophylls based on pooled samples from all three sites (see Methods and Materials for calculation).

Sporophyte recruitment. Recruitment of juvenile sporophytes showed similar patterns at all sites

TABLE 1. Sporophyll fertility.

	2001									2002	
	April	May	June	July	August	September	October	November	December	January	February
Shaw's Cove	5	–	2	–	3	3	4	5	5	5	5
Crystal Cove	0	3	4	–	–	5	2	2	5	5	5
Dana Point	–	0	5	–	–	0	3	3	3	5	5
Mean (%) of fertile sporophylls	50	30	70	0	60	53	60	67	87	100	100

Reported are the monthly numbers of sporophylls with mature sporangial sori based on microscopic examination of sections of five sporophylls from each site ($n = 5$). Dashes indicate month-site combinations where no sporophylls were present on examined *Egregia* axes.

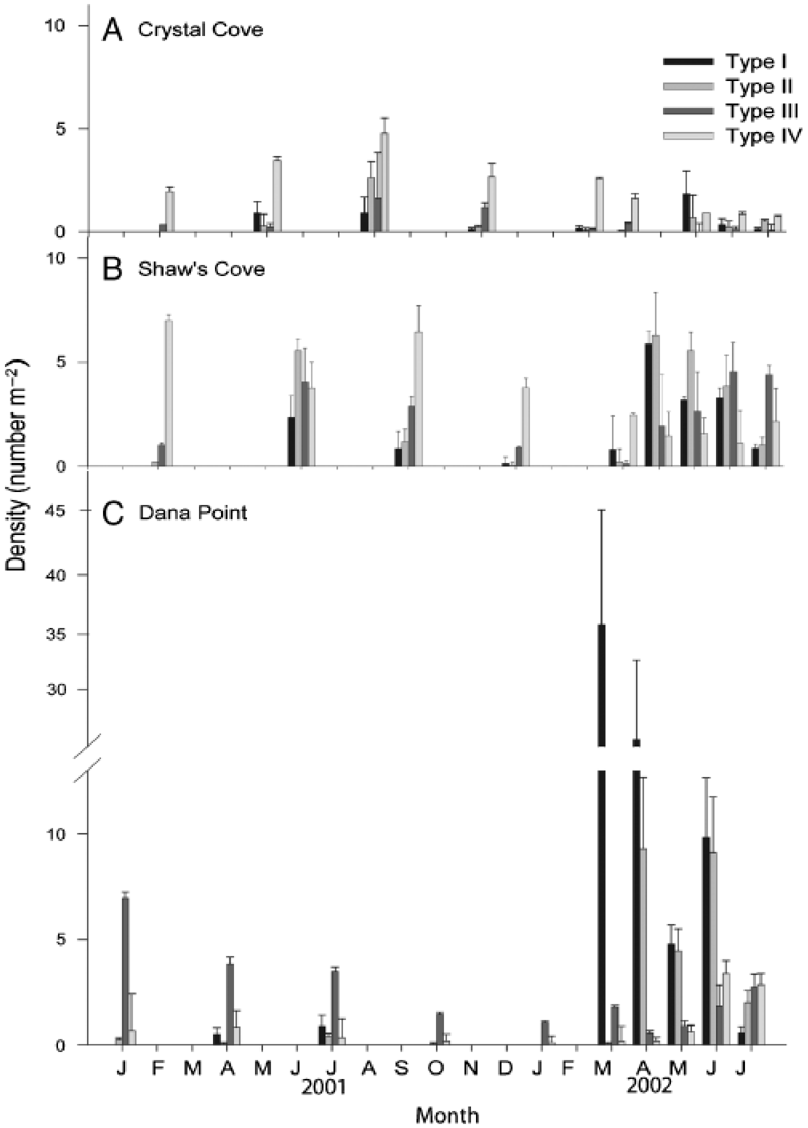

FIG. 6. Seasonal abundances of *Egregia* sporophytes by developmental stage. Plotted are the mean densities (±1 SE) of the four developmental stages (Types I–IV) for the three study sites. Mean values are based on field surveys of plots ($n = 18$) distributed along transect lines.

and between years (Fig. 6), although the intensity of recruitment varied greatly among sites and years. Young (Type I) *Egregia* sporophytes showed peak densities ~5 months following the period of greatest sporophyll production at all sites. Type I thalli appeared in March 2001, were found at all sites through July or August, and then were almost completely absent by the ensuing fall and winter. This pattern was repeated the next year when recruits again became abundant in March 2002 and persisted through July. During 2002, maximum Type I sporophyte recruitment occurred at Dana Point in March ($35.7\,\mathrm{m}^{-2}$) followed by Shaw's Cove in April ($5.9\,\mathrm{m}^{-2}$) and Crystal Cove in May ($1.8\,\mathrm{m}^{-2}$).

Adult sporophyte morphology and herbivore densities. The number of axes in field populations of Type IV (adult) *Egregia* thalli varied significantly among sites but not over time, and a significant interaction between site and season was not detected (Table 2). The average number of axes per Type IV thallus was greatest at Shaw's Cove (16.6±1.5) and least at Crystal Cove (9.5±0.8). The percentage of axes with viable meristems also differed significantly among sites and seasons, and a significant interaction between site and season was observed (Table 2). Despite having more axes per Type IV thallus, *Egregia* from Shaw's Cove had the lowest average percentage of axes with intact meristems compared with thalli at Dana Point or Crystal Cove. As supported by the significant interaction, the percentage of viable axes (with meristems) increased at Shaw's Cove from July through December but dropped at Dana Point during the same period.

TABLE 2. Number of axes and percentage of axes with viable meristems for Type IV *Egregia* sporophytes.

	Sampling period			
Site	January–February	April–June	July–September	October–December
Number of axes				
Crystal Cove	9.3 ± 1.6	8.5 ± 1.4	11.4 ± 1.9	8.8 ± 1.1
Shaw's Cove	14.0 ± 1.6	13.1 ± 3.0	13.2 ± 3.4	21.5 ± 4.0
Dana Point	12.4 ± 2.0	15.4 ± 2.0	14.9 ± 2.1	11.7 ± 1.9
Two-way ANOVA	df	MS	*F*	*P*
Site	2	0.436	6.132	0.003**
Season	3	0.030	0.420	0.743 ns
Site × season	6	0.133	1.871	0.087 ns
% Viable axes				
Crystal Cove	47.5 ± 3.9	61.0 ± 7.3	51.5 ± 5.7	50.5 ± 6.7
Shaw's Cove	33.1 ± 3.7	39.0 ± 7.2	61.1 ± 5.3	42.7 ± 5.0
Dana Point	50.4 ± 4.7	64.9 ± 4.6	49.7 ± 5.1	36.4 ± 5.6
Two-way ANOVA	df	MS	*F*	*P*
Site	2	0.177	3.274	0.039*
Season	3	0.213	3.930	0.009**
Site × season	6	0.174	3.211	0.005**

$^{**}P<0.01$; $^{*}P<0.05$; ns, not significant ($P \geq 0.05$).

Reported are mean values (±1 SE) for each of the three study sites based on 12–22 replicates for the indicated sampling periods. Values for axis numbers were log 10 transformed before analysis of variance (ANOVA).

TABLE 3. Maximum axis lengths for Type IV *Egregia* sporophytes.

Site	January–February	April–June	July–September	October–December
Crystal Cove	2.53 ± 0.35	2.76 ± 0.35	2.72 ± 0.26	1.34 ± 0.19
Shaw's Cove	0.39 ± 0.04	0.37 ± 0.03	0.55 ± 0.04	0.50 ± 0.05
Dana Point	1.43 ± 0.15	1.42 ± 0.14	1.92 ± 0.23	1.58 ± 0.13
Two-way ANOVA	df	MS	*F*	*P*
Site	2	50.020	192.376	<<0.001***
Season	3	1.532	5.891	<0.001***
Site × season	6	0.750	2.885	0.010**

$^{***}P<0.001$; $^{**}P<0.01$; ns, not significant ($P \geq 0.05$).

Reported are mean values (±1 SE) based on 12–22 replicates for each of the three study sites for the indicated sampling periods. Annual mean is calculated as the grand mean of the four period means. Analysis by two-way analysis of variance (ANOVA) with site and season as fixed factors. Values for axis lengths were transformed using the Box-Cox procedure before ANOVA.

Maximum axis lengths varied significantly among sites and seasons, and a significant interaction was found between these fixed factors (Table 3). *Egregia* thalli were much shorter at Shaw's Cove throughout the year (mean = 0.45 m±0.02 m) than thalli collected from Dana Point (mean = 1.57 m±0.07 m) and Crystal Cove (mean = 2.42 m±0.16 m). Maximum axis lengths were more varied at Crystal Cove and, unlike thalli at Shaw's Cove and Dana Point, were much shorter during October to December than previous seasons at the conclusion of the study.

As expected, densities of *N. norrisi* and *Strongylocentrotus* spp. varied among sites (Table 4). Purple urchin ($51.8 \pm 3.9\,\mathrm{m}^{-2}$) and kelp snail ($2.2 \pm 0.2\,\mathrm{m}^{-2}$) densities were much greater at Shaw's Cove, the site with the shortest and more-profusely branched *Egregia* thalli and with the lowest percentage of viable axes. Densities of these herbivores were much lower at Dana Point, where purple urchins ($1.5 \pm 0.7\,\mathrm{m}^{-2}$) and kelp snails ($<0.1 \pm <0.1\,\mathrm{m}^{-2}$) were uncommon, and at Crystal Cove, where kelp snails were rare ($<0.1 \pm <0.1\,\mathrm{m}^{-2}$) and urchins absent from the immediate study area. Numbers of *N. insessa* inhabiting *Egregia* thalli also varied among sites (Table 4). Much higher numbers of *N. insessa* per *Egregia* axis, as well as densities (number per axis cm^{-1}), were found at Crystal Cove compared with the other two sites.

Patterns of lateral morphology. The percentages of spatulate laterals varied significantly by site ($F_{2,285} = 109.8$, $P<0.001$) but not by season ($F_{11,285} = 1.6$, $P = 0.10$), and an interaction between site and season was not detected ($F_{22,285} = 1.3$,

TABLE 4. Herbivore densities.

	Crystal Cove	Shaw's Cove	Dana Point
Strongylocentrotus pupuratus Stimpson, 1857	0	51.8 ± 3.9	1.5 ± 0.7
Strongylocentrotus franciscanus A. Agassiz, 1863	0	0.1 ± <0.1	< 0.1 ± <0.1
Norrisia norrisi Sowerby, 1938	< 0.1 ± <0.1	2.2 ± 0.2	< 0.1 ± <0.1
Notoacmaea insessa Hinds, 1842	2.3 ± 0.9	< 0.1 ± <0.1	0.7 ± 0.3

Reported are mean densities (number · m^{-2}) ±1 SE of urchins (*Strongylocentrotus* sp.) and kelp snails (*Norrisia norrisi*) for the three study sites based on averages over all monthly site visits ($n = 9$–10). Reported for *Notoacmaea insessa* are the number of individuals per *Egregia* axis averaged over all monthly collections ($n = 90$–103 per site).

$P = 0.13$; Fig. 7a). The percentage of filiform laterals similarly varied significantly by site ($F_{2,286} = 122.8$, $P<0.001$) and additionally varied by season ($F_{11,286} = 3.6$, $P<0.001$), declining in winter during the period of greatest sporophyll production; again, an interaction between site and season was not found ($F_{22,286} = 1.2$, $P = 0.24$; Fig. 7b). Spatulate laterals were more prevalent basally, with intermediate laterals becoming more common on longer axes. Finally, filiform laterals became increasingly abundant with axis length and were most profuse apically. Thus, shorter axes had predominately spatulate laterals, and longer axes bore higher numbers of intermediate and filiform laterals.

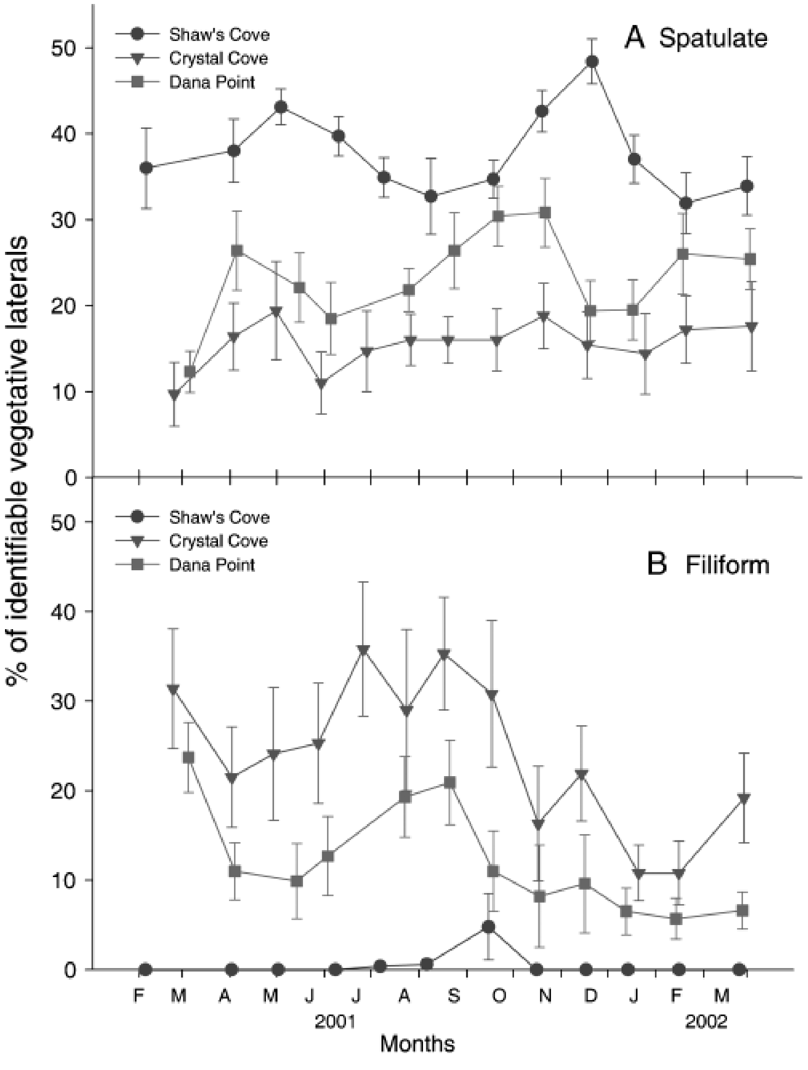

FIG. 7. Monthly patterns of *Egregia* lateral morphology at three sites. Values are the percentage (±1 SE) of spatulate (A) or filiform (B) of the total identifiable vegetative laterals for the indicated sampling periods.

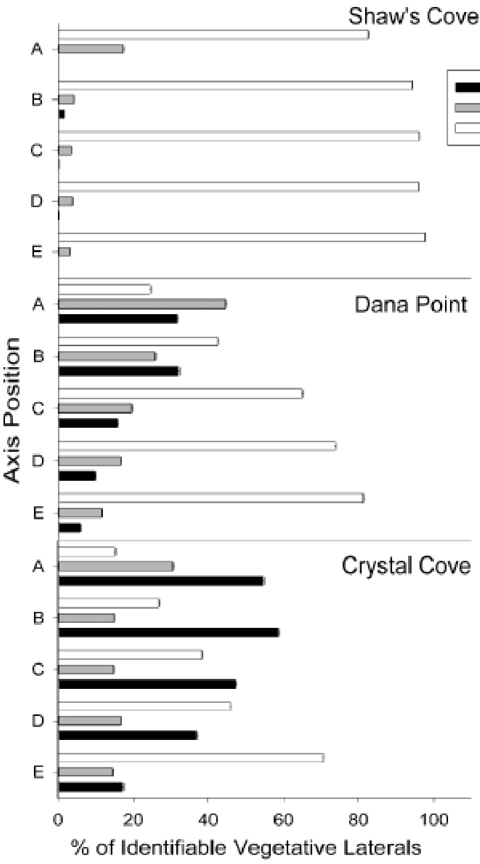

FIG. 8. Lateral morphology by axis position. (A) Shaw's Cove. (B) Dana Point. (C) Crystal Cove. Plotted are percentages (+1 SE) of identifiable vegetative laterals for filiform, spatulate, and intermediate morphs by axis location based on the indicated number of sampled thalli. Axis positions (A–E) are defined in the Methods and Materials and represent a gradient from the meristem (A) to the basal (E) part of the axis.

At Shaw's Cove, where the axes collected for morphological analysis were shortest (0.66 ± 0.02 m), thalli almost exclusively produced spatulate laterals and generally bore only a few intermediate laterals, which were located mostly near growing meristematic tips (Fig. 8a). At Dana Point, where axes of intermediate length (1.14±0.05 m) were collected, intermediate and filiform laterals were found in the highest percentages at the distal ends near the meristems; most axes, however, possessed spatulate laterals, particularly at their basal regions (Fig. 8b). Filiform laterals dominated the upper (distal) half of the longer axes (1.29±0.05 m) collected from Crystal Cove; but, as was the case at both Shaw's Cove and Dana Point, basal portions of axes retained mostly spatulate laterals (Fig. 8c).

Photosynthesis and respiration. Rates of net photosynthesis and dark respiration varied significantly among *Egregia* thallus parts ($F_{4,49} = 63.8$, $P_{\mathrm{psn}} < 0.001$; $F_{4,49} = 16.4$, $P_{\mathrm{resp}} < 0.001$; Fig. 9). As hypothesized, filiform laterals had significantly higher light-saturated net photosynthetic rates ($9.8 \pm 0.1\ \mathrm{mg\,O_2 \cdot g^{-1} \cdot h^{-1}}$) than any of the other lateral types. Intermediate ($7.6 \pm 0.1\ \mathrm{mg\,O_2 \cdot g^{-1} \cdot h^{-1}}$) and spatulate ($6.8 \pm 0.1\ \mathrm{mg\,O_2 \cdot g^{-1} \cdot h^{-1}}$) laterals formed a subset with statistically indistinguishable rates, which were greater than the rates exhibited by the sporophylls ($2.9 \pm 0.1\ \mathrm{mg\,O_2 \cdot g^{-1} \cdot h^{-1}}$). The rachis ($0.8 \pm <0.1\ \mathrm{mg\,O_2 \cdot g^{-1} \cdot h^{-1}}$) had the lowest photosynthetic rate of any incubated thallus part. Dark respiration rates also differed significantly among thallus parts (Fig. 9). Among vegetative laterals, dark respiration rates of the filiform ($1.2 \pm 0.1\ \mathrm{mg\,O_2 \cdot g^{-1} \cdot h^{-1}}$) and intermediate ($1.1 \pm 0.1\ \mathrm{mg\,O_2 \cdot g^{-1} \cdot h^{-1}}$) laterals were highest and statistically indistinguishable. Intermediate rates of respiration were observed for the sporophylls ($0.9 \pm 0.1\ \mathrm{mg\,O_2 \cdot g^{-1} \cdot h^{-1}}$), and the lowest rates were found for spatulate laterals ($0.5 \pm 0.1\ \mathrm{mg\,O_2 \cdot g^{-1} \cdot h^{-1}}$) and the rachis ($0.4 \pm <0.1\ \mathrm{mg\,O_2 \cdot g^{-1} \cdot h^{-1}}$).

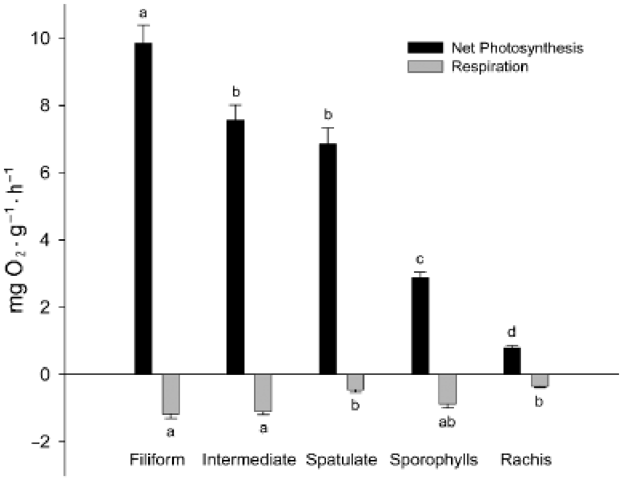

FIG. 9. Light-saturated net photosynthesis and dark respiration rates for *Egregia* thallus parts. Plotted are means (+1 SE) based on 9–12 replicates. Letters represent statistically significant subsets of means based of Student-Newman-Keuls' test results.

DISCUSSION

Southern California populations of *E. menziesii*, like many perennial macroalgae occurring outside the tropics, exhibited a strong seasonal pattern of reproduction. These results are consistent with previous reports (Abbott and Hollenberg 1976, Gordon and De Wreede 1978) of seasonal peaks in *Egregia* fertility. Similar to *Egregia* from Santa Barbara (Black 1974, 1976), the Southern California *Egregia* populations in this study showed greatest sporophyll production and sorus fertility from December through February, when monthly SSTs averaged 11–13°C. Similar results were observed for *Egregia* from British Columbia (Gordon and De Wreede 1978), where summer temperatures of 10 and 15°C coincided with greatest production of gametophytes and sporophytes, and winter temperatures of 7°C depressed gametophyte and sporophyte development. Furthermore, Myers (1928) found that the male gametophytes would not release their antherozooids at temperatures of 16°C or greater. Other reports (Abbott and Hollenberg 1976) indicate that in California, *Egregia* produces sporophylls between April and November. Although we observed much greater fertile sporophyll production during winter, small numbers of sporophylls, some of which were fertile, were detected throughout the year, reinforcing the suggestion (Abbott and Hollenberg 1976) that *Egregia* can be reproductive year-round. We did not investigate the roles of spore production and germination success, however, and seasonal differences in these parameters could significantly affect the reproductive patterns derived soley from sporophyll production. With this qualification, the reproductive pattern observed for *Egregia* in this study appears to be similar to that observed for *Macrocystis pyrifera* (L.) C. Agardh (Neushul 1963, Anderson and North 1967, Reed et al. 1996) and *Laminaria saccharina* (L.) Lamour. (Druehl and Hsiao 1977, Lee and Brinkhuis 1986), species which also show seasonal peaks in spore production but can be reproductive year-round. Unlike Southern California populations of *Egregia*, however, both *M. pyrifera* and *L. saccharina* exhibit a second peak in spore production during the year, with spore germination success varying greatly between the two periods (Deysher and Dean 1986). The single, strong reproductive period found in *Egregia* also resembles the narrow reproductive window observed in *Pterygophora californica* Rupr., although this kelp produces spores only from November through April regardless of environmental conditions (Reed et al. 1996).

Reproductive effort can be determined by measuring the proportion of thallus biomass allocated to reproductive tissues (Chapman 1985); however, such calculations are difficult to perform and must be interpreted with caution in kelps and other seaweeds where many very small reproductive cells are produced in sori (Santelices 1990). Nevertheless, the amount and seasonal pattern of biomass allocated to reproductive tissue in *Egregia* (14.9% of dwt in January to 0.6% in July) were similar to reports (Novaczek 1984) for *Ecklonia radiata* (C. Ag.) J. Ag. (17% frond surface area covered with sori in winter to 0.2% in summer), another member of the Alariaceae. Our values, however, are higher than those reported for *M. pyrifera* (4%; Neushul 1963) and lower than reports for *Laminaria* sp. (2%–30%; Kain 1971, 1975, Perez 1971, DeWreede and Klinger 1988), *Ascophyllum nodosum* (L.) Le Jol. (40%–60%; Cousens 1986), and other fucoids (80%–90% of the deciduous fronds; Santelices 1990). It is unlikely that the winter peak in the proportion of reproductive biomass observed for Southern California *Egregia* populations is due to winter biomass loss (as has been reported for *Macrocystis*; Graham 2002, 2003) because minimum axis lengths were found in the spring at two of the three sites, and there was no significant difference among seasons for the number of axes per thallus.

Maximum sporophyll production in our *Egregia* populations occurred during winter conditions of shorter days and coldest ocean temperatures (Fig. 5). Other studies also provide support for a cold temperature requirement for successful *Egregia* reproduction. Spores released from *Egregia* collected in northern California in the fall and cultured under conditions of 10–18°C produced gametophytes and completed the life history by giving rise to new sporophytes in 19–28 days (Myers 1928). In contrast, material collected in summer and cultured under warmer ambient temperatures (16–20°C) produced gametophytes but failed to give rise to new sporophytes (Myers 1928). Moreover, the optimum temperature for the onset of gametophyte fertility in Southern California *Egregia* is 12°C, and gametophyte fertility was inhibited at 20°C (Lüning and Neushul 1978).

As expected for algae (Hoffmann and Santelices 1991), especially species with distinct gametophyte and sporophyte stages, we observed a lag between the period of greatest fertile sporophyll production by *Egregia* and the detection of new sporophyte recruits in the spring. We measured the greatest recruitment of juvenile *Egregia* sporophytes from March through June, 5 months following the time of maximum sporophyll and, presumably, spore production. This peak was similar to the spring maxima in *Egregia* sporophyte recruitment reported for other Southern California sites, including La Jolla (Gunnill 1980, 1985) and San Clemente Island (Murray and Littler 1977, 1978), but later than that observed in Santa Barbara, California, where new sporophyte generations recruited from January to March (Black 1974, 1976).

Intertidal populations of *Egregia* exhibit a life history strategy in Southern California that appears to be timed to coincide with optimal conditions for reproductive success. *Egregia* produces sporophylls and releases its spores following the summer period of greatest growth (Black 1974) and during stressful winter periods when the lower of the mixed semidiurnal low tides occurs in the afternoon (Seapy and Hoppe 1973, Seapy and Littler 1982, Littler et al. 1991). Hypothetically, the few-celled gametophytes produced during this period are able to develop in microhabitats protected from desiccation under the cold water temperatures required for optimizing fertility (Myers 1928, Lüning and Neushul 1978). The spring recruitment of vulnerable juvenile sporophytes takes place later in the year when the timing of lower tides shifts toward the early morning, and lower shore habitats occupied by *Egregia* are emersed for only brief periods (Seapy and Hoppe 1973, Littler et al. 1991). Spring recruits of *Egregia* at the three sites appeared to reach reproductive maturity in 6–7 months, as evidenced by observations during the fall of sporophylls present on young, newly recruited thalli <50 cm in length. Reproduction in the first season is common in intertidal kelps because, although they are potential perennials, the vast majority behave as annuals under stressful intertidal conditions (Druehl and Hsiao 1977).

The highly seasonal winter peak in sporophyll production and spring peak in sporophyte recruitment suggest that reproductive success in intertidal *Egregia* is influenced by environmental conditions during these critical periods. For example, abnormally warm, winter ocean temperatures might reduce *Egregia* sporophyll production and gametophyte fertility. Moreover, algal propagules and early postsettlement stages are known to experience high mortality under a variety of abiotic and biotic conditions (Vadas et al. 1992), and kelp gametophytes and microsporophytes are highly vulnerable to burial and scour by sediments (Neushul et al. 1976, DeVinny and Volse 1978, Dayton et al. 1984) and to grazing pressure (Kain and Jones 1966). The large discrepancy between the high number of fertile *Egregia* thalli and the ensuing small number of young sporophyte recruits suggests that postsettlement survival of gametophytes and young sporophytes is crucial to maintaining *Egregia* populations at our study sites.

Our studies are the first to demonstrate that variations in lateral morphology can be related to axis length and provide a possible mechanism for the development of different lateral morphologies on the same *Egregia* thallus. Variations in the morphology of *Egregia* laterals have long been recognized (Setchell 1893) and were previously used as a basis for discriminating species and varieties within the genus (Chapman 1962a). Lateral morphologies in *Egregia* show strong geographic patterns: both broad, spatulate, and narrow, filiform laterals occur on Southern California thalli (Abbott and Hollenberg 1976), whereas narrower and thicker spatulate laterals commonly occur north of Point Conception, California (Blanchette et al. 2002). Results for our Southern California *Egregia* populations, however, reveal a possible developmental basis for variation in lateral morphology on the same thallus. Filiform laterals became the dominant morph on longer axes, whereas spatulate morphs characterized young, short thalli and persisted on the older, basal regions of more mature and longer plants. This pattern of form variation in *Egregia* is unlike that in other kelps where differentiation in stipe morphology (Mann 1971, Chapman 1973), the amount of blade bullation (Armstrong 1987, Roberson 2001), the length-to-width ratios and thickness of the blades (Parke 1948, Sundene 1962a, b, 1964, Svendensen and Kain 1971, Palmisano and Sheng 1977, Gerard and Mann 1979, Gerard 1987, Miller and Dorr 1994, Miller et al. 2000), or changes in the internal morphology (Burrows 1964) have been associated with environmental factors, such as growing depth, wave exposure, or temperature gradients. However, our observations for Southern California might not apply to *Egregia* populations in more northerly geographic regions where thallus and lateral morphologies can be more variable.

Perhaps because of observations that lateral morphologies can vary on the same thallus, Chapman (1962a) hypothesized that filiform laterals arise from narrow leaflets that develop proliferations or that with increasing age broader blades become eroded and proliferated. However, we observed that filiform laterals developed directly on the distal ends of longer axes, a finding that contradicts Chapman's hypotheses. Chapman (1962a) additionally reported that shallow, wave-exposed forms of *Egregia* with short thalli had axes covered with broad laterals and hypothesized that the shorter life span of these smaller, heavily buffeted individuals prevented complete erosion of the leaflets. Alternatively, we attribute this dominance of broad, spatulate laterals on shorter *Egregia* axes to developmental patterns and not to the absence of blade erosion.

The form of an algal thallus is known to correlate with nutrient-uptake abilities (Odum et al. 1958), photosynthetic and respiration rates (Kanwisher 1966, Littler and Murray 1974, King and Schramm 1976, Littler 1980, Littler and Littler 1980, Littler and Arnold 1982), and possibly susceptibility to herbivory (Littler and Littler 1980, but see Padilla and Allen 2000). Differences in photosynthetic and respiration rates for different stages of development and different parts of *Egregia* thalli have been reported previously. For example, whole, young *Egregia* thalli had net photosynthetic rates that were ~2.5 times the rates of fully differentiated adult thalli (Littler and Littler 1980, Littler and Arnold 1982). Similarly, variations in photosynthesis to respiration ratios (Clendenning and Sargent 1958) and in net photosynthetic rates (Druehl 1984) have been observed for different thallus parts in *Macrocystis*.

The results of the photosynthesis experiments supported earlier studies conducted by Chapman (1962b) and confirmed that net photosynthetic rates of filiform laterals are greater than spatulate laterals. Our studies also indicate that, per meter of axis, filiform-laden fronds of *Egregia* are 12% more productive than spatulate-covered fronds, given the higher photosynthetic rates and greater concentrations of filiform ($15.8\,\mathrm{cm}^{-1}$) versus spatulate ($6.9\,\mathrm{cm}^{-1}$) laterals on *Egregia* thalli. Interestingly, this observation contradicts results of an earlier Southern California study (Littler and Arnold 1982) where upper thallus segments consisting of filiform laterals were 32% less productive than basal portions with blade-like laterals of the same thalli. However, reduced rates for upper segments might have been caused by large numbers of low-producing sporophylls because Littler and Arnold's photosynthetic experiments were performed during October when, according to our studies, Southern California *Egregia* thalli show a sharp increase in sporophyll production.

Egregia menziesii is distributed across a broad latitudinal range in the eastern North Pacific where it shows considerable variation in its vegetative and reproductive morphology (Abbott and Hollenberg 1976). Variation in the vegetative lateral blades of *Egregia* has long been recognized but poorly explored. Our results indicate a developmental basis for variation in blade morphology in Southern California populations of *Egregia*; blades transitioned from lower densities of broader, spatulate laterals to higher densities of thinner, filiform laterals with increasing axis length. These changes increase the productivity of longer *Egregia* axes and, based on additional studies by Henkel (2003), also make the lateral blades of longer *Egregia* fronds less susceptible to molluscan herbivores. Sporophylls, which in our Southern California *Egregia* population ranged from furrowed, raisin-like forms to flattened structures with wrinkled bases, were fertile year-round but were much more abundant during winter periods of colder ocean temperatures. Peak sporophyte recruitment occurred in spring, about 5 months following the period of greatest sporophyll production, suggesting a temporal link between these events. Reproductive patterns in *Egregia* likely vary, however, north of Southern California where cooler ocean conditions occur throughout the year. Additional studies are needed to describe morphological variation and reproductive periodicity across the latitudinal range of *Egregia* and to determine the degree to which environmental factors affect observed patterns in this common and often abundant kelp.

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In Pursuit of Bio-Criteria for Evaluating the Condition of Rocky Intertidal Communities

Report of a Workshop Sponsored by the University of Southern California Sea Grant Program with Assistance from the Bureau of Ocean Energy Management, Regulation and Enforcement

Steven N. Murray, Pete Raimondi, and Stephen B. Weisberg

Introduction

The ecological communities of California's rocky coast are being altered by the combined impacts of coastal development, pollution, climate change, and visitor activities. Previous research has revealed that these rocky intertidal communities are dynamic and show change in response to natural (e.g., wave action, sand scour, substratum instability) and anthropogenic (e.g., effluent discharges, trampling) disturbance. Coastal managers are concerned with the status of these coastal ecological communities and are often charged with implementing procedures that protect and enhance species composition, diversity, and ecological services. They are faced with an increasing need to evaluate and monitor community change and performance, particularly with the current focus on Ecosystem-Based Management (EBM) and the implementation of the Marine Life Protection Act (MLPA). A key need is the ability to distinguish anthropogenic-driven changes in a coastal community from changes due to natural or non-anthropogenic agents. Coastal managers are seeking the metrics to determine the current condition or "health" of a site and trends in this condition over time, and to communicate this condition to the public and decision-makers in a simple manner. Ideally, this would include metrics that can be collected by citizen-scientists as well metrics or sets of metrics that can be collected by highly trained individuals. Moreover, these metrics need to be collected in a resource-limited environment. However, the development of simple metrics that reflect the condition of rocky intertidal communities has remained elusive due to the complex, dynamic, and heterogeneous nature of rocky shore ecosystems (Murray et al. 2006).

Work needs to be done to determine if parameters can be identified that represent the status of rocky shore ecosystems so monitoring and evaluation can be focused, informative, and easily communicated. Biocriteria or biotic indices have long been utilized for this purpose to evaluate the status of aquatic and terrestrial ecosystems. These criteria or indices translate environmental or biotic data into an index value or a grade, thereby breaking down complex information into an easily understandable scoring system. For example, the Index of Biological Integrity (IBI) has been employed to assess ecosystem condition in streams (Karr 1991) and soft-bottom, benthic (Weisberg et al. 1997) habitats and, similarly, the Terrestrial Index of Ecological Integrity (TIEI) has played a similar role in terrestrial ecosystems (Andreasen et al. 2001). Weisberg et al. (2008) indicate that recognized European and U.S. approaches to developing biocriteria for assessing ecological systems include: 1) comparison to historical conditions; 2) comparison to present reference conditions; 3) models; and, 4) consensus (or best) professional judgment (BPJ). Rice (2003) lists the following categories of ecosystem indicators: 1) Indicator Species; 2) Diversity Indices; 3) Multivariate Ordination Techniques; and, 4) Aggregated Indicators of Ecosystem Status, and also discusses indicators that move beyond these categories and, with the aid of an ecological model, reflect emergent ecosystem properties. A key question is whether similar biocriteria or biotic indices can be developed that accurately represent the status of rocky shore ecosystems and that capture the degree to which rocky intertidal communities are disturbed by natural or anthropogenic agents.

To address this question, a team of rocky intertidal experts was convened and a three day workshop held on March 5-7 2010 at the Wrigley Institute for Environmental Science on Santa Catalina Island, California. They were joined by coastal managers and administrators of agencies and programs interested in monitoring changes in rocky intertidal populations and communities. The workshop was sponsored by the University of Southern California Sea Grant program with assistance from the Bureau of Ocean Energy Management, Regulation and Enforcement. A list of workshop participants is provided in Table 1.

Table 1. Workshop Participants

Rocky Intertidal Experts

Rich Ambrose *University of California, Los Angeles*
Carol Blanchette *University of California, Santa Barbara*
Jennifer Burnaford *California State University, Fullerton*
Megan Dethier *University of Washington, Friday Harbor Laboratories*
Jack Engle *University of California, Santa Barbara*
Mike Foster *Moss Landing Marine Lab*
Melissa Miner *University of California, Santa Cruz*
Steve Murray *California State University, Fullerton*
Karina Nielsen *Sonoma State University*
John Pearse *University of California, Santa Cruz*
Pete Raimondi *University of California, Santa Cruz*
Dan Richards *Channel Islands National Park Service*
Christy Bell *University of California, Santa Cruz (Participated in Exercise but did not attend Workshop)*
Jayson Smith *California State University, Fullerton*

Managers

Dominic Gregorio *State Water Resources Control Board*
Mary Elaine Helix *Bureau of Ocean Energy Management, Regulation and Enforcement*
Cheri Recchia *Marine Monitoring Enterprise*
Steve Weisberg *Southern California Coastal Water Research Project*
Elizabeth Whiteman *Marine Monitoring Enterprise*

Workshop Facilitators

Phyllis Grifman *University of Southern California, Sea Grant Program*
Susan Zaleski *University of Southern California, Sea Grant Program*

The specific goals of the workshop were: 1) to determine whether there would be a high level of agreement among experts in identifying disturbed (natural and anthropogenic) rocky intertidal sites using only species abundance data and meta-data describing physical site characteristics; and, 2) if so, whether these experts would make their identifications using similar approaches. An ultimate goal of the workshop was to determine which characteristics of species abundance data sets were useful for distinguishing disturbance levels for rocky intertidal sites and whether it might be possible to use these characteristics to develop criteria or an index that reflect the disturbance status of rocky intertidal populations and communities. If developed, this index will be of great benefit to managers of California's parks, beaches, and shoreline, as well as those responsible for discharges into Areas of Special Biological Significance (ASBS), who often face difficulties in determining benchmarks for evaluating the effectiveness of their management strategies.

Prior to the workshop, a group of rocky intertidal experts was identified and asked to participate in an exercise to evaluate the condition of rocky intertidal sites using uniform data sets. This exercise was modeled after one performed for benthic infaunal communities where experts used their best professional judgment to assess the condition of 35 California soft bottom sites working only from blind data sets (Weisberg et al. 2008). In this exercise, participating experts ranked sites in a highly correlated way ($r = 0.91$) and achieved strong agreement on site condition. They also used similar parameters for making their assessments. In this pre-workshop exercise, each rocky intertidal expert was asked to examine common data sets containing the abundances (% cover for macro-invertebrates and macrophytes; density for mobile macro-invertebrates) of intertidal species for 31 site data sets. In addition, meta-data (substratum type, slope, relief, wave climate, sediment influence, shore expanse, and nature of nearby up and down coast habitat), and calculations of total substratum cover and measures of diversity (numbers of taxa, H', J', d, and $1\text{-}\lambda$) were provided for each site data collection. All data sets were obtained from Pete Raimondi and his U.C. Santa Cruz intertidal sampling program.

Investigators were informed that each of the sites was located along a biogeographically uniform portion of the California coastline between Point Conception and Point Reyes. However, specific site locations were not provided and sites were identified only by number. Also unbeknown to the participants, the data included repetitive seasonal visits for five of the sampled sites. Thus, a total of 26 independent sites were investigated with data for 5 of these sites provided for two different sampling periods (Figure 1). No information describing natural disturbance (other than that deduced from the meta-data) and anthropogenic disturbance to sites was made available.

Experts were instructed to use their best professional judgment to conduct any form of analysis they found useful to examine the data and arrive at their conclusions. Each expert was to:

1) Assign each of the 31 site data sets to one of five condition categories – undisturbed, largely undisturbed, neutral, moderately disturbed, strongly disturbed – using the numerical codes for the five-point disturbance scale: undisturbed (1) to strongly disturbed (5);

2) Identify the five site data sets most strongly influenced by anthropogenic disturbance;
3) Describe the criteria (or attributes) used to arrive at the disturbance classifications together with a rating of the importance of each of these criteria; and,
4) Describe the criteria (or attributes) used to identify the five sites most strongly influenced by *anthropogenic* disturbance.

All expert analyses were compiled, presented to the workshop participants, and discussed to determine the degree of agreement in the site classifications and approaches used.

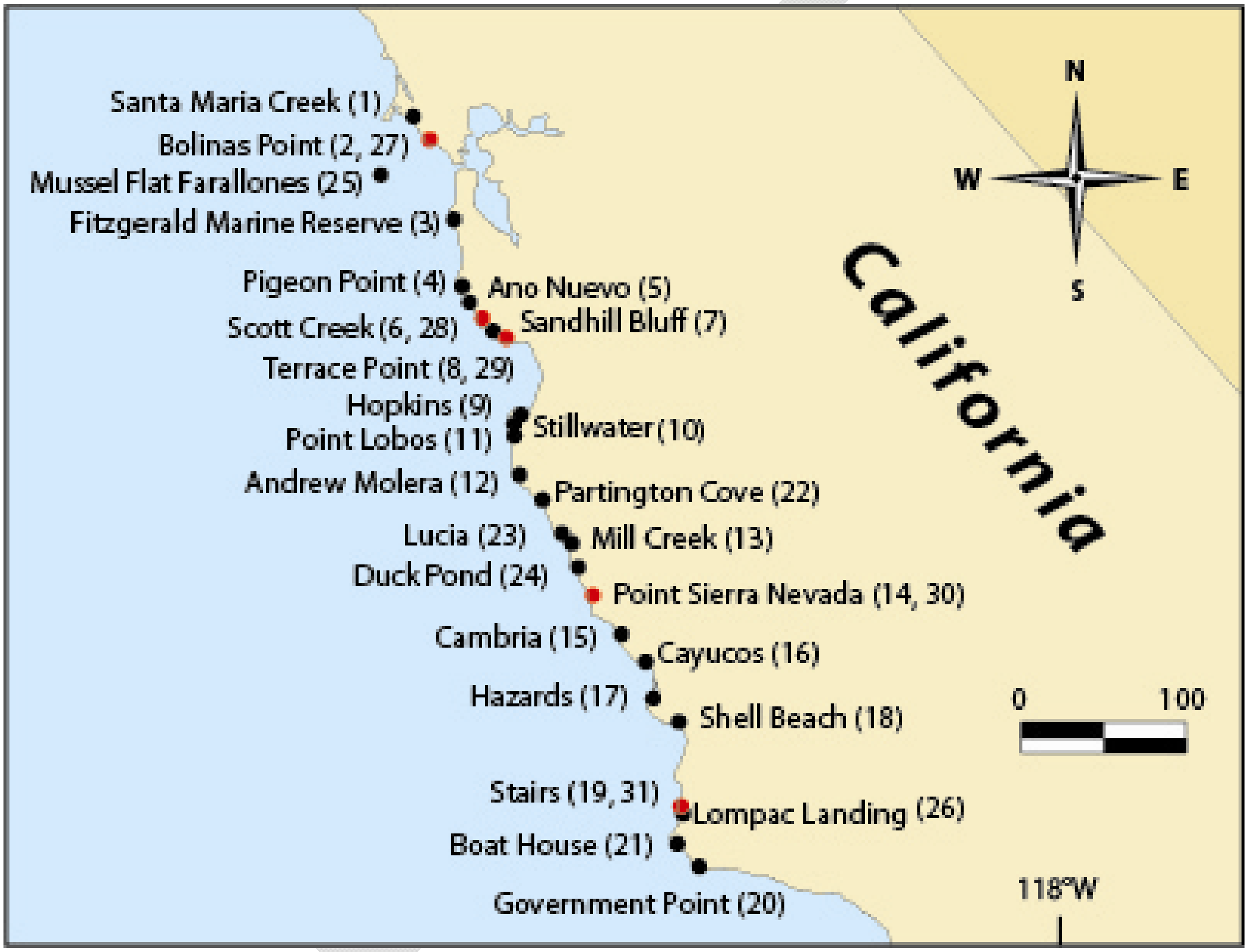

Figure 1. Map depicting the sites and site numbers for which data sets were supplied to experts. Note: experts were provided two temporal data sets for sites denoted by red points on the map.

Results

Identification of the Level of Site Disturbance. There was fairly good agreement among the experts in identifying the sites subjected to the greatest degree of disturbance. However, much less agreement was evident in identifying sites subjected to moderate disturbance or that received little disturbance (Table 2; Figure 2). Four site data sets (7, 8, 24 and 29) received the highest disturbance scores, averaging > 4.00 on the 5.00 scale and for Site 24 all except for one investigator scored this site as "strongly disturbed". The data sets represented two different temporal visits to one of these four intertidal locations (sites 8 and 29). Thus, expert consensus was reached on 3 of the 26 independent sites. The site identified as the next most disturbed based on expert consensus was Site 5, followed by Sites 1, 2, and 23. Eight sites (4, 9, 12, 17, 21, 26, 28, and 30) fell on the undisturbed end of the scale based on expert scores. These sites tallied scores < 2.5. Interestingly, two of these site data sets represented sites with two seasonal visits where the experts scored one visit as less disturbed than the other. No site received more than four scores of 1 ("largely undisturbed").

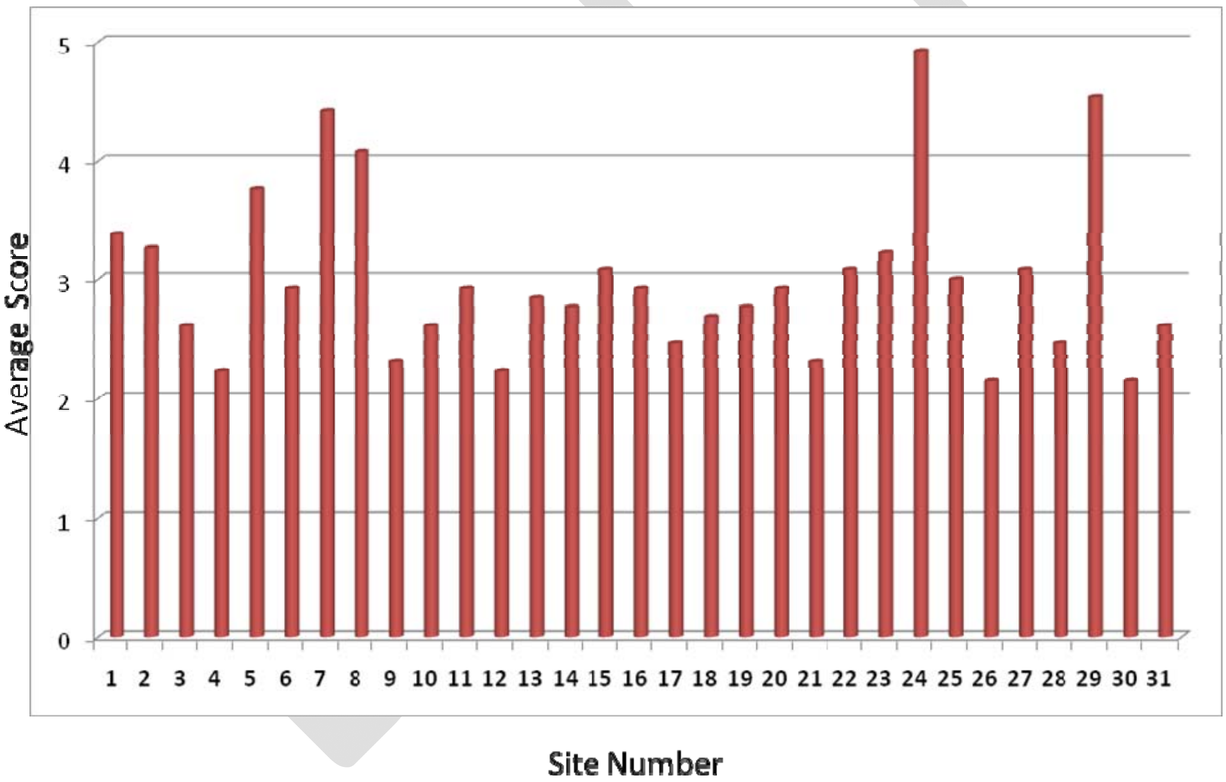

Figure 2. Average score by experts for the 31 site data sets. Sites with two separate temporal visits are 8 and 29, 2 and 27, 6 and 28, 14 and 30, and 19 and 31. Note: 5 = strongly disturbed; 4 =moderately disturbed; 3 = neutral; 2 = largely undisturbed; 1 = undisturbed.

Table 2. Results of disturbance assignments of the 13 experts (A to M). Sites are arranged from top to bottom by average score. Sites with two seasonal visits are 8 and 29, 2 and 27, 6 and 28, 14 and 30, and 19 and 31. Note: 5 = Strongly Disturbed; 4 =Moderately Disturbed; 3 = Neutral; 2 = Largely Undisturbed; 1 = Undisturbed.

Investigator

Site Number	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**	**L**	M	Average
24	5	5	5	5	5	5	5	5	5	5	5	4	5	4.92
29	5	5	5	4	4	5	5	4	3	5	5	5	4	4.54
7	5	5	5	4	4	4	4	4	4	4	5	5	5	4.42
8	5	5	5	4	1	4	4	4	2	4	5	5	5	4.08
5	3	4	4	4	4	4	4	4	4	4	3	3	4	3.77
1	2	4	3	4	3	4	4	2	2	4	4	5	3	3.38
2	3	4	4	4	2	2	3	3	4	4	3	3	4	3.27
23	5	3	4	2	1	4	3	3	2	3	2	5	5	3.23
15	3	5	4	3	2	3	4	3	4	4	3	1	1	3.08
22	5	1	4	2	1	5	4	3	2	2	1	5	5	3.08
27	3	4	3	4	2	1	2	3	4	2	5	4	3	3.08
25	4	3	4	3	1	1	3	4	2	2	3	4	5	3.00
6	2	3	4	3	3	4	2	3	2	2	4	4	2	2.92
11	1	2	4	3	2	5	3	4	5	3	2	2	2	2.92
16	4	3	4	3	1	2	4	3	4	3	2	1	4	2.92
20	1	3	4	3	1	4	3	3	4	2	2	5	3	2.92
13	1	4	4	3	2	4	3	3	4	2	3	2	2	2.85
14	1	4	2	3	2	4	3	3	4	3	2	3	2	2.77
19	1	4	2	3	1	3	2	4	4	3	3	2	4	2.77
18	1	4	4	3	1	3	3	3	4	2	3	1	3	2.69
3	3	1	4	3	2	2	4	3	4	2	3	1	2	2.62
10	1	3	3	2	2	4	4	3	2	3	1	3	3	2.62
31	1	2	2	3	1	3	2	4	4	3	3	2	4	2.62
17	1	1	2	4	4	2	1	3	4	1	3	3	3	2.46
28	2	4	2	3	2	1	1	3	3	1	4	4	2	2.46
9	3	4	4	2	1	1	2	3	4	1	2	1	2	2.31
21	1	2	3	3	1	3	3	3	2	3	2	2	2	2.31
4	3	3	4	2	1	1	3	2	3	2	3	1	1	2.23
12	3	2	2	3	1	3	3	3	2	2	2	2	1	2.23
26	1	2	3	2	1	2	1	3	2	3	1	4	3	2.15
30	1	1	2	3	1	2	2	3	3	3	2	3	2	2.15

A problem identified in the score assignments during workshop discussions was that experts were interpreting polar ends of the disturbance scale differently, i.e., investigators differed in their interpretations of what was a Strongly Disturbed Site that merited a 5 score or an Undisturbed Site that merited a 1 score. Hence, even though investigators might similarly rank sites by levels of disturbance they might assign different numerical scores.

Identification of Sites Most Strongly Influenced by Anthropogenic Disturbance. Experts found it difficult to distinguish anthropogenic from natural or non anthropogenic-driven disturbance. Nevertheless, fairly good agreement was reached among experts in the identification of the most anthropogenically disturbed sites (Figure 3).

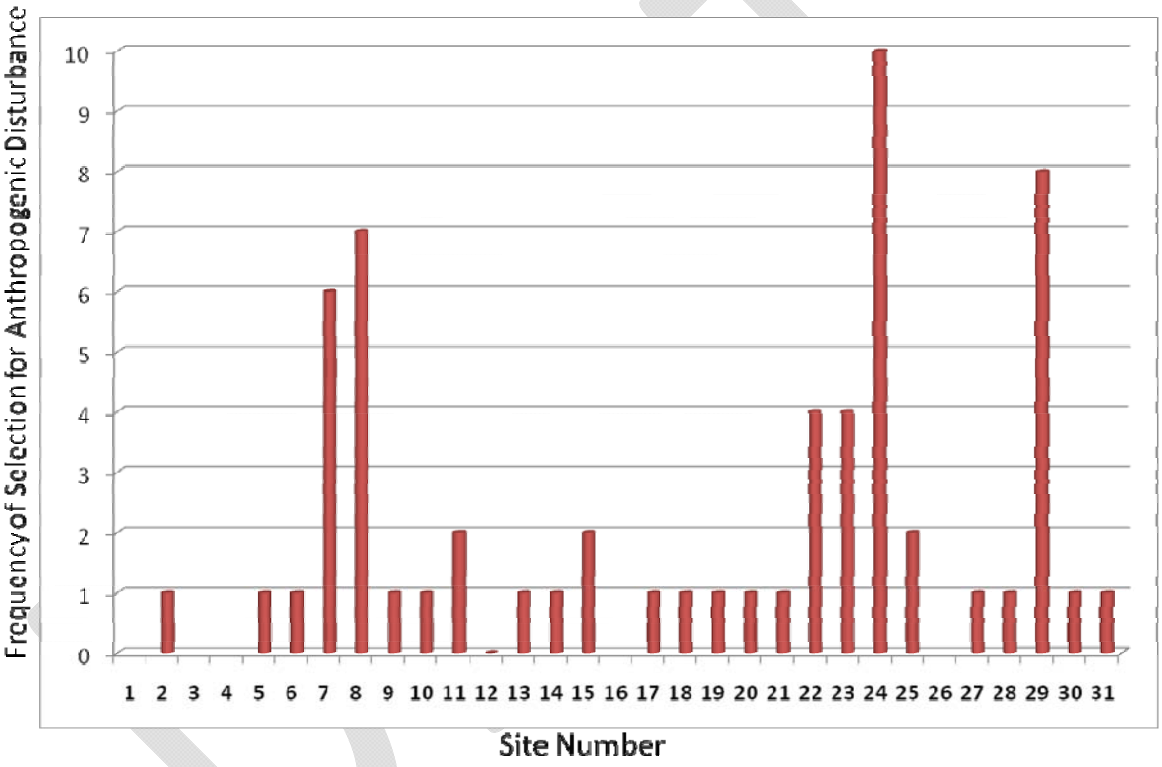

Figure 3. Frequency of identification of site data sets most influenced by anthropogenic disturbance by the 13 experts. Each expert Identified the 5 site data sets believed to be those most subjected to anthropogenic disturbance.

The site most frequently identified by experts to be impacted by anthropogenic disturbance was site 24. Sites 29, 8, and 7 were also often identified as being subject to anthropogenic disturbance followed by sites 22 and 23. Interestingly, all but 6 sites were named by at least one expert as being among the five most disturbed by human influence. Of the 25 listed sites, 16 sites were identified by only one of the 12 experts that submitted results for this portion of the exercise.

The most frequently identified sites (29, 24, 7, 8) were also the sites considered by the experts to be the most disturbed regardless of whether disturbance stemmed from natural or anthropogenic sources. In fact, there was a strong correlation (r = 0.88) between the average score for a site on the five point disturbance scale and the frequency with which a site was identified as being disturbed by anthropogenic agents (Figure 4).

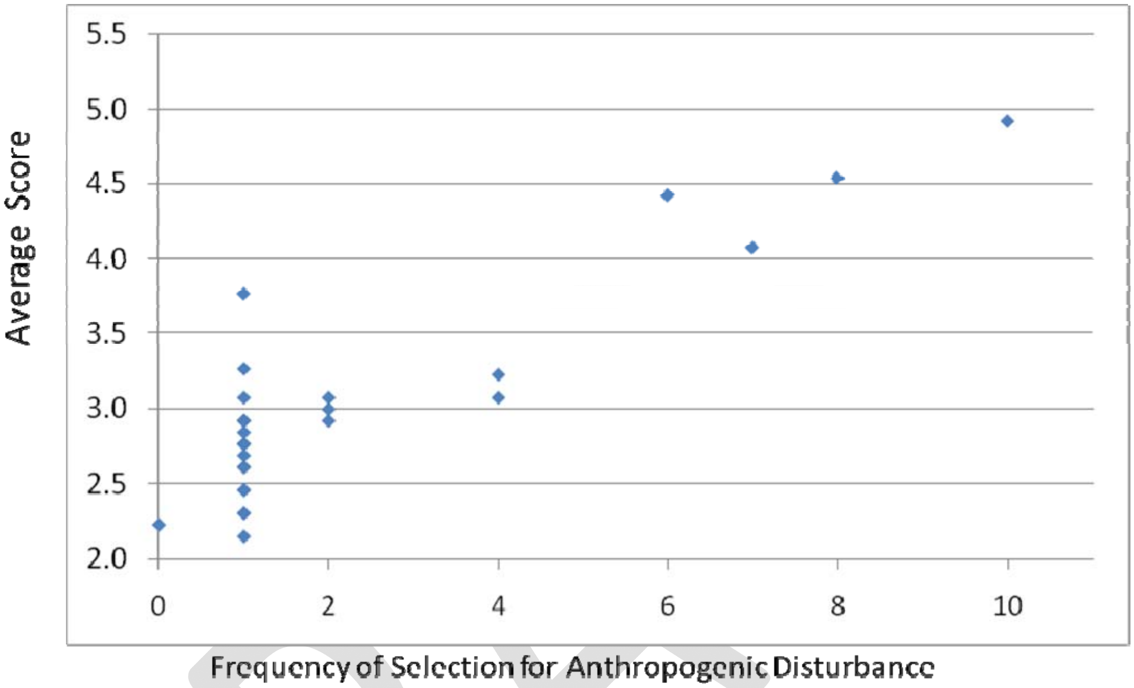

Figure 4. Correlation between the average scores for a site based on the five-point disturbance scale and the frequency with which a site was identified by experts as being among the five sites most subjected to anthropogenic disturbance. Five of the 26 independent sites were not identified as being among the top five subjected to anthropogenic disturbance.

<u>Approaches Used by Experts to Place Sites on a Disturbance Scale.</u> Working solely from the provided data, experts used a variety of approaches and criteria to identify the degree of disturbance, regardless of source, affecting each of the 31 site data sets. No guidance was given so each expert's approach and decision-making was independent. Nevertheless, there was a high degree of similarity in the key criteria identified by experts in making their evaluations of site disturbance. The approaches and criteria used can be condensed into five categories (Table 3). These were consistent with the criteria and approaches used previously (see Rice 2003) to assess ecosystem condition and included: 1) ordination methods drawing on the full use of all biotic data, e.g., community-level analyses using multivariate statistics; 2) the relative cover of biota and bare rocky substratum; 3) the abundance profiles of specific species populations and types of species; 4) community diversity; and 5) the prevalence of selected physical factors. Most experts used multiple criteria in developing their site disturbance scores.

Table 3. Summary of approaches and criteria used by experts to identify the degree of disturbance, regardless of source, affecting site data sets.

Approach or Criteria	Examples
Community-Level Analyses	Cluster Analysis and MDS mostly using cover data
Overall Cover Patterns	Disturbance Indicators: Low Biotic Cover; High Bare Rock Cover
Diversity	Disturbance Indicator: Low Diversity (Numbers of Taxa, H', 1-λ, Family Richness)
Abundances of Species Groups or Selected Taxa	Disturbance Indicators: High Cover of Opportunistic Seaweeds (e.g., *Ulva*, Filamentous, Sheet, and Tubular Algae); Low Cover of Rockweeds; High Abundances of Mussels, Sea Stars, Limpets; Low Abundances of Black Abalone, Sea Grasses, and Corticated Algae; Absence of Certain Species; Deviations from Expected Abundance Patterns
Physical Factors	Disturbance Indicator: High Sand Cover or Scour; High Wave Exposure; Unstable Substratum (e.g., Cobble)

Approaches Used by Experts to Identify the Sites Most Subject to Anthropogenic Disturbance. Experts uniformly expressed concern about identifying the 5 sites most subject to anthropogenic disturbance among the 31 site data collections examined and in identifying the criteria used. Of principal concern was the ability to distinguish between natural and anthropogenic disturbance and the acknowledgement that multiple disturbance agents affect rocky intertidal sites so distinguishing natural from anthropogenic drivers becomes problematic. Two other issues arose during discussions of the identification of anthropogenically-disturbed sites. The first was that there appeared to be a narrow range of anthropogenic disturbance affecting the sites examined in the exercise. This could be addressed by including sites that represented a wider range of site types with respect to anthropogenic disturbance in a subsequent exercise. The second was that biological parameters are affected differently by different types of anthropogenic disturbance. Hence, it is difficult to key in on data indicators without knowing the type of anthropogenic disturbance. Experts agreed that addressing this topic requires more study and work.

Exercise Challenges. There were two primary exercise challenges identified during the workshop discussions:

1) Experts used variable definitions of "disturbance". Some considered "natural" disturbance part of the natural state of a system, so a site with high levels of wave action, for example, was considered by some to be not very disturbed because this is part of its natural state. Whereas, participants, using this same information, categorized this type of site as highly disturbed. The definition of "natural" disturbance and how one categorizes this disturbance is essential for creating an index that represents site condition and reflects anthropogenic driven changes from the expected natural state.

2) Experts variously interpreted the thresholds separating the five assessment categories when scoring the degree of disturbance. The scale for ranking sites from 1 to 5 was

not clearly defined, so this left room for individual expert interpretation. For example, some experts failed to rank any site as "largely undisturbed", whereas others assigned "strongly disturbed" rankings to only one site in the exercise. As a consequence, while good agreement was reached on the most disturbed sites, much less agreement was achieved in the disturbance scores for less disturbed sites and the inter-investigator correlation (r = 0.34) established from expert scores was relatively low. Participants agreed that with clearer more uniform interpretations of the five point disturbance scale, much better agreement would likely be realized.

Deviations from Expected Site Conditions. Rocky intertidal habitats vary greatly from site to site based on biogeography and physical site features, including exposure to non-anthropogenic forms of natural disturbance. Experts agreed that these factors must be addressed in order to develop an index that describes the status of a site with respect to anthropogenic impact. In this exercise, sites were located within a uniform biogeographic region to eliminate geographic changes in biota such as between central and southern California. Physical variations in site features (e.g., wave exposure, sand influence, and substratum type, slope, and relief) were present and needed to be accounted for by experts in making their assessments. Thus, the challenge for making a determination of site condition and the degree to which a site was exposed to anthropogenic disturbance was to evaluate the suite of biological characteristics (e.g. species abundances, diversity, etc.) against what was believe to be the expected condition. Then, deviations from this expected condition could be used to assess site status. This approach would enable managers to identify sites that have drifted from expected conditions but would not determine causality. This approach requires understanding of:

1) Normal variation expected within each site type
2) The ends of the spectrum along the site condition scale
3) Past or current conditions used to set the end of the spectrum where the site was free from anthropogenic influences.

Future Work. Given the progress made at this workshop, the participants agreed that a follow-up exercise and ensuing workshop would be productive. Participants concluded that the ratings of a site data set were more based on differences in how an expert defined and categorized disturbance and determined the disturbance level on the five-point scale compared with the actual data-based characterization of the site. A principal purpose of a follow-up exercise would be to overcome interpretational differences among experts in rating sites and to make further progress in identifying the metrics that could best be used to describe site condition. This will require discussion of the expected biological characteristics of sites under different types and degrees of environmental "disturbance". The follow-up exercise should be similarly constructed, including data from a range of sites unknown to the experts and should include additional, strongly disturbed site data sets to provide a wider range of conditions to evaluate. In addition, the disturbance scale should be more clearly defined to reduce the variation in a score given to a site data set viewed similarly by experts in terms of disturbance level. In this follow-up exercise, experts should also be asked to rank sites from first to last on the more clearly defined disturbance scale.

Summary of Consensus Outcomes. The results of the workshop were promising and several consensus outcomes were realized. In summary these were:

1) Rocky intertidal habitats vary greatly from site to site based on non-anthropogenic environmental drivers making simple assessments of the status of these sites complex;
2) There are some common characteristics and approaches that experts used to come up with their assessments of each site;
3) Definitions are needed to clearly articulate what is meant by “disturbance”, including anthropogenic driven “disturbance”;
4) The scale for scoring disturbance, including its end points, needs to be clarified to eliminate noise resulting from investigator interpretation;
5) Once “natural” environmental characteristics are accounted for, sites would be expected to display a suite of biological characteristics (e.g. species abundances, diversity, etc.) that would represent the expected condition and then deviations from this expected condition could be used to describe site status;
6) Establishing an index to capture the condition of rocky intertidal sites appears feasible and is worth pursuing.

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Consistent Frequency of Color Morphs in the Sea Star *Pisaster ochraceus* (Echinodermata : Asteriidae) across Open-Coast Habitats in the Northeastern Pacific[1]

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Abstract: The sea star *Pisaster ochraceus* (Brandt, 1835) is among the most conspicuous members of northeastern Pacific rocky-shore fauna due to its dramatic color variation, ranging from bright yellowish orange to brown to deep purple. Despite a large body of ecological and developmental biology information on *P. ochraceus*, few studies have rigorously examined color patterns or their causes across its geographic range. We used thousands of observations of sea star color and size taken from southern California to northern Oregon to show that the frequency of orange sea stars is approximately 20% with little variation across a broad latitudinal band. However, the frequency of orange sea stars in a population increases with the size of the animals in most populations. We consider several alternative hypotheses for these color patterns but find that the most parsimonious explanation is that adult color is a selectively neutral genetic trait that expresses itself ontogenetically. These novel findings point to the need for renewed study of the basic biology of this key ecological species.

One of the most immediately conspicuous observations in northeastern Pacific tide pools is the striking color differences in the sea star *Pisaster ochraceus* (Brandt, 1835). Even at a distance one can easily pick out orange and purple sea stars as they line the rock walls near intertidal mussel beds. Anecdotally, experienced intertidal biologists have observed that about one-fourth to one-third of the *P. ochraceus* in any given site along the open Pacific coast are orange, and the remainder are some variant of brown, rust, or purple (E. Sanford, J. Pearse, R. Strathmann, and C. Harley, pers. comm. to R.D.S. 2004). Although *P. ochraceus* is one of the most extensively studied intertidal invertebrates, with many published studies, for example, on its development (George 1999), physiology (Vasu and Giese 1966), diet (Feder 1959, Menge 1972), effects on prey species (Mauzey et al. 1968), parasitism (Leighton et al. 1991), settlement patterns (Sewell and Watson 1993), role as a "keystone" species (Paine 1966, Menge et al. 2004) and in maintaining alternate community states (Paine and Trimble 2004), and reactions to climatic change (Sanford 1999), remarkably little is known about the basic biological foundations of its color variants nor the ecological conditions that support phenotypic color polymorphism in this sea star. Most of what we know about color morphs in *P. ochraceus* stems from studies done more than half a century ago on small numbers of individuals from just one or two locations.

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Fox and Scheer (1941) confirmed that color in *P. ochraceus* is determined by two carotenoid pigments, suggesting that diet plays a role in coloration because animals generally do not produce carotenoids. Beyond that paper, an unpublished study of variation in color polymorphism by Forbes (1951), and a review by Fox and Hopkins (1966), none of the 128 published works on *P. ochraceus* indexed by ISI Web of Knowledge between 1910 and 2005 nor the citations on *P. ochraceus* reviewed in *Intertidal Invertebrates of California* (Morris et al. 1980) addressed color patterns in *P. ochraceus* or the mechanisms for them.

Phenotypic color polymorphism in other organisms has been commonly observed (Endler 1986, Galeotti et al. 2003, Wente and Phillips 2003) and has generated numerous evolutionary explanations for why sometimes strikingly different colors should be maintained. In almost all studies, the null hypothesis that color polymorphism is selectively neutral has been rejected. Although color polymorphism without an obvious selective mechanism is unexpected, it is not unprecedented. Oda and Ishii (2001) demonstrated that color polymorphism in *Conocephalus maculatus* katydids is genetically determined but not under environmental selection, and Finke (1994) found no sexual, apostatic, or disruptive selective mechanisms acting on female color dimorphism in *Enallagma* damselflies.

Alternative hypotheses generally can be classified as invoking either selective mechanisms that have a persistent effect on populations or transient mechanisms that rely on a phenotypically plastic trait. Alternative hypotheses with empirical support based on selective mechanisms include (1) nonrandom mating due to sexual selection or signaling to prevent inbreeding (Houde 1987, Galeotti et al. 2003); (2) apostatic selection, in which rare morphs are more successful in hunting prey or avoiding predators through the disruption of search images or advertisement of distastefulness (Allen 1988, Gillespie and Oxford 1998, Horth 2004); (3) disruptive selection through crypsis in heterogeneous backgrounds or physiological adaptation to spatially or temporally variable environments (Nevo 1973, Hairston 1979, Etter 1988); and (4) balancing trade-offs among these agents. Mechanisms invoking plasticity include the roles of (1) color plasticity in response to environmental factors (Wente and Phillips 2003); (2) dietary differences resulting in phenotypic differences (Tlusty and Hyland 2005); and (3) ontogenetic color change (Booth 1990).

With so many potential mechanisms, it may not be logistically feasible to study color polymorphism in a species across a large range using detailed mechanistic experiments such as those used on smaller scales or on easily manipulated study systems (e.g., laboratory experiments with guppies). However, a common theme to almost all alternative hypotheses is that color morphs are segregated into different spatial, temporal, ontogenetic or behavioral niches for which the different color morphs are better adapted. This suggests that broad-scale observations of color morphs taken across an environmental gradient containing many of these niches, combined with an understanding of the natural history of an organism, can begin to eliminate the likelihood of certain hypotheses while suggesting more-likely hypotheses that could be addressed with specific mechanistic studies. Here we use an unprecedented number of color and size observations obtained over a wide latitudinal gradient to examine alternative hypotheses related to the maintenance of color polymorphism in *P. ochraceus*.

MATERIALS AND METHODS

Samples of *Pisaster ochraceus* size and color were taken by three different groups of investigators that share data as part of the Multi-Agency Rocky Intertidal Network (MARINe) and the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO). Samples were taken biannually between fall 2000 and fall 2003 at 26 sites located between southern California (33.71° N) and northern Oregon (45.92° N) within permanent demarcated plots in the low intertidal (Figure 1). Sizes of the plots varied with site, ranging from 20 to 160 m^2, depending on geomorphology and available habitat. Because our goal was

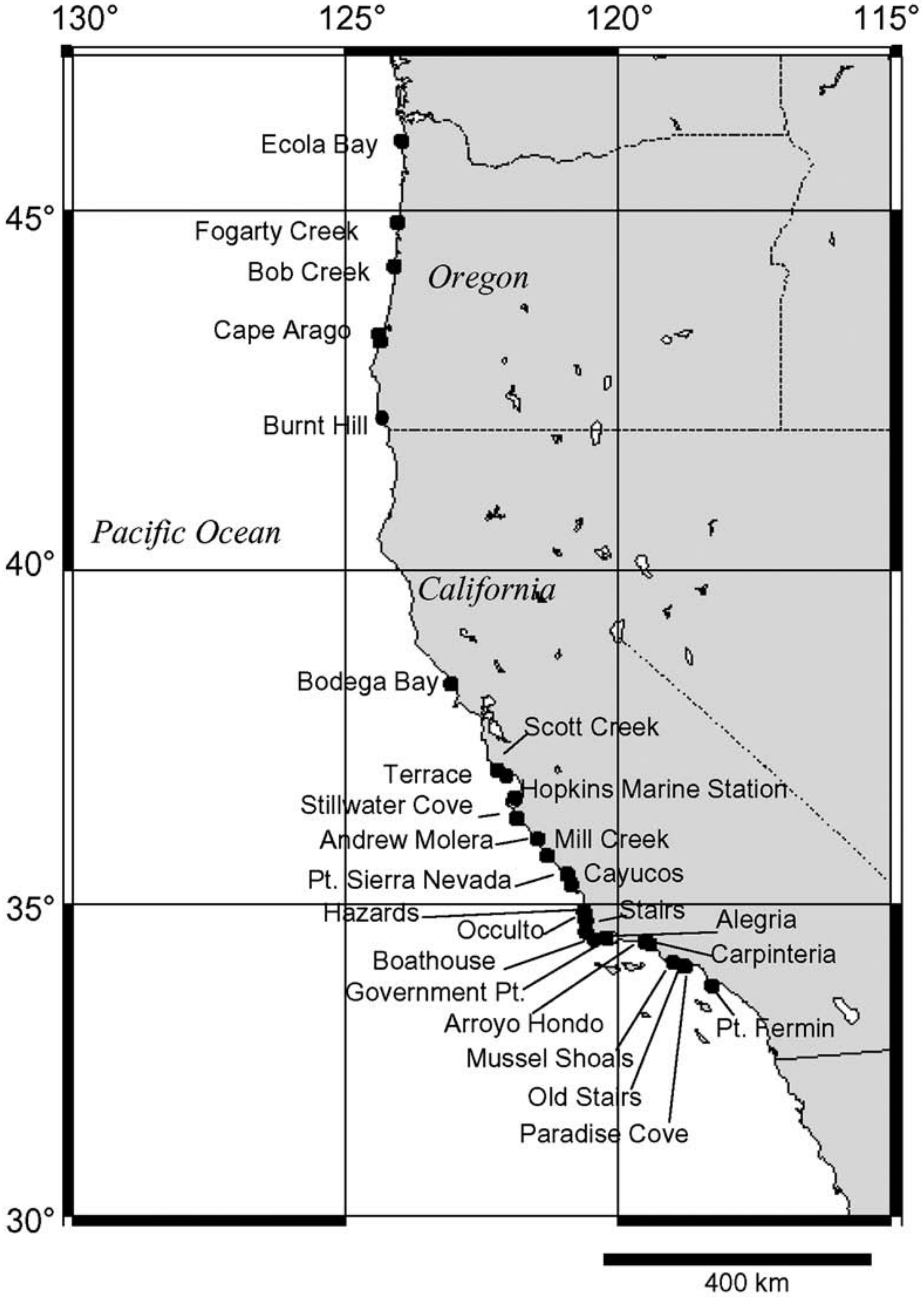

Figure 1. Map of 26 study sites along the west coast of North America.

specifically to measure and record the color of many individuals at each site, plots were chosen to represent a range of habitat types (e.g., low intertidal crevices, rock walls, and pools) where *P. ochraceus* of all postsettlement life stages can be found, rather than a stratified random plot design (which would be more appropriate if the goal was to compare population size estimates).

Sites were sampled by MARINe researchers from University of California, Los Angeles (UCLA), and the University of California, Santa Cruz (UCSC), and PISCO researchers from UCSC. Because our sampling methodology is relatively simple and was conducted by experienced intertidal researchers who frequently communicate about sampling issues, differences due to observer bias in recording color or size across sites is unlikely.

Our study sites are wave-exposed open coast areas that represent the most common *P. ochraceus* habitat over most of its geographic range. We also used additional observations by ourselves and others from protected-water sites in Puget Sound (Washington State) and Vancouver Island, British Columbia, to gain insight into the open-coast patterns we report. Along the 1,850-km stretch of open coast from Baja California to Oregon, and farther north, sea stars generally occur in orange, purple, and brown color morphs. All sampled sea stars were measured and scored for color as either "orange" or "purple" (all brown and darker shades were scored in the "purple" category because field tests determined that brown and purple forms are difficult to differentiate consistently). Although there is considerable color variation among the darker forms in this species, we use this simple orange/purple dichotomy in our observations and analysis because it is least likely to introduce sampling bias while still offering the ability to evaluate the orange color morph patterns observed in the field.

Size measurements were made with calipers or rulers from the tip of the longest arm to the center of the aboral disk and recorded to the nearest 10 mm. Pilot data from 438 individuals confirmed a strong correlation between this radial measurement and oral disk radius (Pearson correlation coefficient = 0.879, $P < .001$) and width of the largest arm (Pearson correlation coefficient = 0.904, $P < .001$), indicating that maximum radius is representative of size.

Our analysis was designed to focus on color ratios and to avoid issues of nonindependence that might arise from repeatedly sampling individuals in permanent quadrats. Hence, at each site we calculated the percentage of orange individuals for each sample period and then averaged those percentages to produce an overall site average. To examine the percentage of orange individuals in populations of different sizes the mean number of purple and orange individuals for each 10-mm size bin across all sample periods was calculated for each site. Means were then summed for these color categories across all sites and the percentage of orange morphs was calculated. By aggregating our data, the potential problem of near-zero or zero values in the smallest and largest size categories was avoided.

Finally, habitat use, aggregation by color, and seasonal differences in color ratios were tested using quantitative analyses (chi square and analysis of variance [ANOVA]), specialized data collection efforts, and through qualitative observations made during sampling visits.

RESULTS AND DISCUSSION

The monitoring data analyzed here, incorporating 14,720 observations of *Pisaster ochraceus*, demonstrate both consistency of orange color frequencies in adult sea stars over a broad latitudinal gradient (Figure 2) and changes in the frequency of orange morphs from small to large sea stars at most sites (Figure 3). The range in percentage orange morphs for all sites was 12.6–27% (mean = 20.0 ± 4.4% SD). Regression of percentage orange against size was positive and highly significant ($R^2 = 0.74$, $P < .001$).

Observations of 177 individuals from Hopkins Marine Station (central California) and Old Stairs (southern California) showed no relationship between color and habitat type (flat benches, vertical walls, or shaded crevices) (Pearson chi-square = 1.38, df = 2,

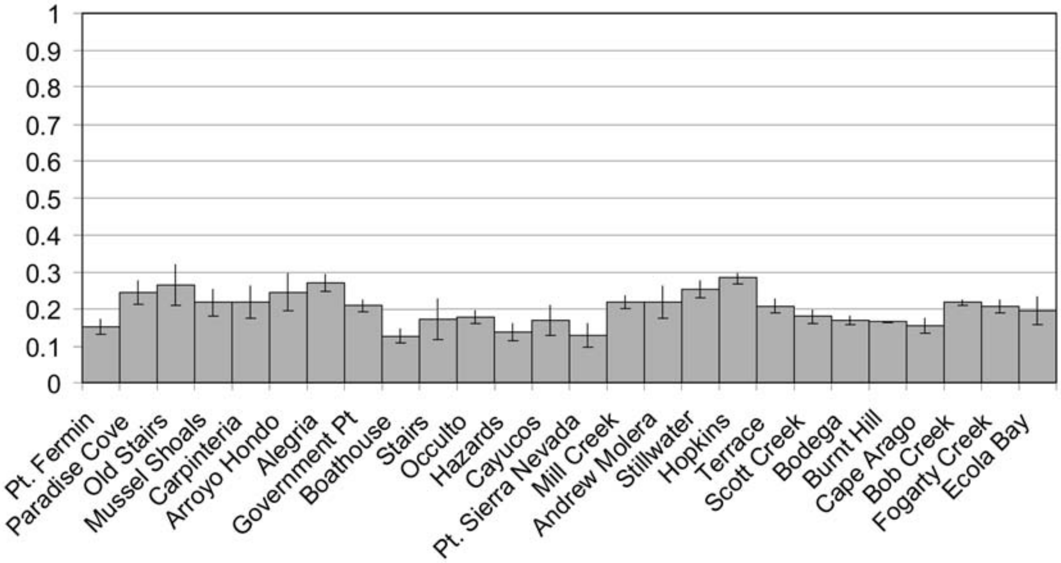

Figure 2. Average percentage of orange sea stars (±SE) in the population at all sites, arranged from south to north.

$P = .501$). Similarly, clustering of color morphs was not detected because 24% of nonorange sea stars were found closest to orange individuals and 78% of orange sea stars, mirroring the overall color frequencies, were found closest to nonorange sea stars. These results are in accordance with qualitative observations of the frequency of color morphs in this species that we made during hundreds of sampling visits. Finally, we found no evidence of consistent seasonal differences in the percentage of *P. ochraceus* orange color morphs in our sampled populations (ANOVA, $F = 1.09$, df $= 45$, $P = .364$).

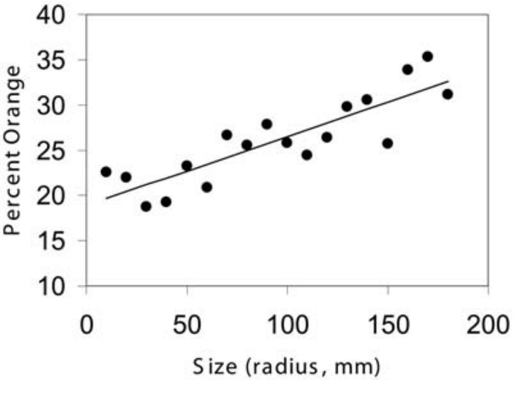

Figure 3. Percentage of orange sea stars in increasing size bins. The mean number of purple and orange individuals for each 10-mm size bin across all sample periods was calculated at each site. Means were summed for each color across all sites and percentage orange was calculated.

Selective Mechanisms

The wealth of knowledge on *P. ochraceus* raises doubts about hypotheses that invoke selective mechanisms as viable explanations for color polymorphism in this species. These sea stars are dioecious, broadcast spawners with little visual ability beyond sensing light and dark (Morris et al. 1980). Hence, it is unlikely that color serves as a cue for sexual or other forms of visually based selection. The sea star's main prey items are sessile and use only size as an escape from predation, or use their mobility to escape by responding to chemical traces of the predator in the water (Phillips 1975, Morris et al. 1980). Thus, color differences would not afford any color morph an advantage in obtaining prey.

Among larger (>30-mm radius) individuals, no *P. ochraceus* color morph is cryptic in intertidal habitats. Greater mortality in purple *P. ochraceus* could lead to an increase in the frequency of orange sea stars in a population. However, predation on sea stars is not commonly observed, although sea otters prey on *P. ochraceus*, and seagulls are occasionally observed pulling sea stars off intertidal rocks. If relying on visual cues (whether color or monochromatic), these visual predators would likely target the more conspicuous orange sea stars, which contrast more strongly with the coloration patterns of intertidal habitats. Although it is plausible that experience with sea stars or some color-specific olfactory signal could impart a preference for purple stars if orange stars are less palatable, to date no one has investigated this hypothesis. However, as Ricketts and Calvin (1939:116–117) explained, "*Pisaster* neither has nor seems to need protective coloration. Anything that can damage this thoroughly tough animal, short of the 'acts of God' referred to in insurance policies, deserves respectful mention."

Across the geographic range of our study sites, intertidal communities experience widely different climatic conditions, tidal regimes, and species assemblages, and yet the ratio of orange morphs to other color variants remains similar. Moreover, the different color morphs of *P. ochraceus* do not segregate into different niches—spatially, temporally, or behaviorally. Our observations collected over 120 sampling visits, as well as those of numerous intertidal ecologists, suggest that color morphs do not separate into different intertidal habitats, nor do they aggregate preferentially, or show a seasonal component to color dominance. These observations were supported by our more-detailed scoring of habitat use and aggregation by color at Hopkins Marine Station and Old Stairs sites, as well as the quantitative analysis of our data parsed by season. Finally, populations appear to be well mixed genetically across their range. Recent work by Harley et al. (in press) revealed no geographic genetic population structure across the species range, even when comparing locations on alternate sides of known biogeographic boundaries or known discontinuities in larval supply. These findings suggest that genetic drift is not likely to play a dominant role in affecting color morph frequencies.

Nonetheless, a limited temporal and spatial perspective could mask selective pressures affecting these populations. For example, subtidal populations, which were not sampled, could have different overall color ratios due to selective pressures on color. However, this appears even less likely than in intertidal habitats because *P. ochraceus* would be less affected by environmental conditions such as heat stress while immersed and coloration could only be affected by selective sea otter predation at the small number of our sites supporting otter populations. Alternately, color polymorphisms observed at one time may be under selection toward the dominance of one form (e.g., Stolz et al. 2003). The samples we analyzed do not represent a time series long enough to determine conclusively if the observed color ratios vary over time. However, observations of color ratios of 1,327 *P. ochraceus* (across all sizes) by biology student Clifford Forbes in 1951 indicated orange frequencies of 20% in Trinidad, California (41.07° N), and 25% at Hopkins Marine Station (36.62° N) (Forbes 1951), mirroring the values we observed in our samples.

Size-Related Plasticity

The size-related shift in the frequency of orange color morphs, which has not previously been documented, seems to indicate phenotypic plasticity in this trait. The color shift could arise from diet, ontogenetic differences in mortality, or ontogenetic color change. Adults of both color morphs were consistently observed congregating on the same prey items (e.g., *Mytilus californianus*). Feder (1959) demonstrated that regardless of geographic location or habitat, *P. ochraceus* overwhelmingly eats the prey it is primarily found with, suggesting that these sea stars feed primarily on the California mussel (*M. californianus*) throughout its range. Nonetheless, *P. ochraceus* also will feed opportunistically on many other prey items in our study range

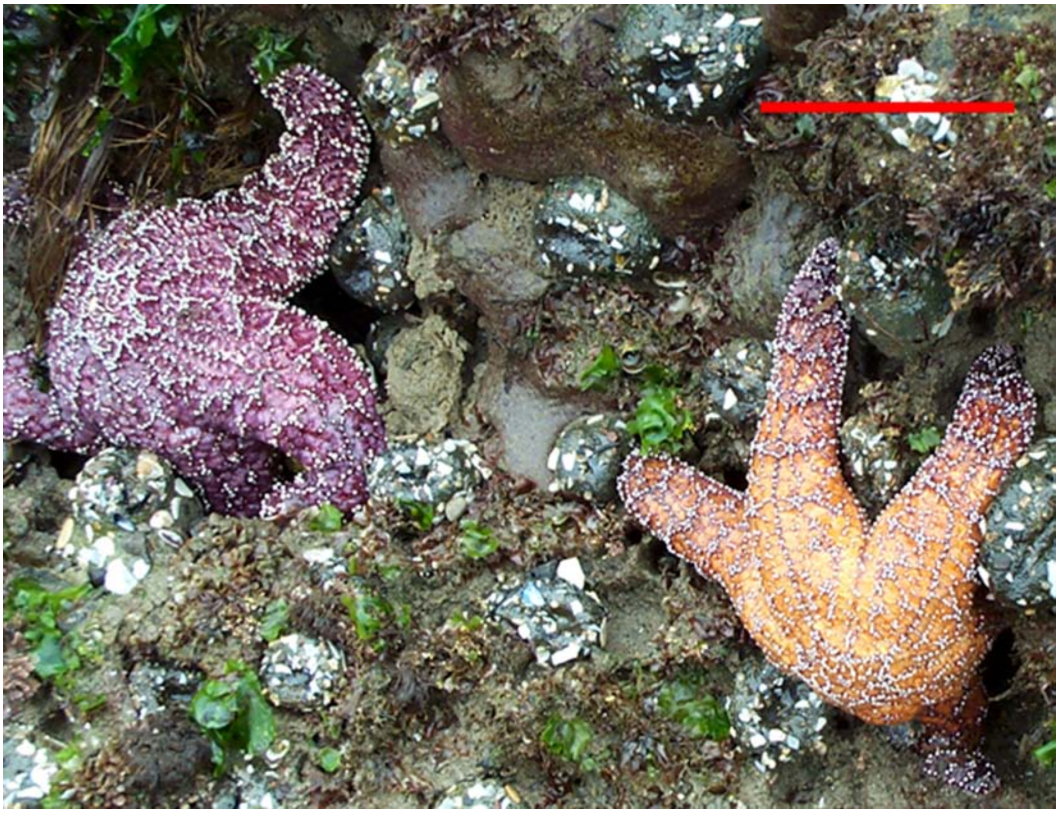

Figure 4. Purple (*left*) and orange (*right*) *Pisaster ochraceus* photographed at low tide at Carpinteria, California, March 2004, by R.D.S. Scale bar approximately 10 cm. Note purple (dark) arm tips on the orange sea star.

(E. Sanford, pers. comm. 2006). Although it is conceivable that mussels of different quality (e.g., reproductive individuals) might affect color or that alternative prey items might impart different color pigments to their predators, it is not clear how (or why) only one sea star color morph would consistently target one type of mussel or alternative food source. However, food sources of juvenile *P. ochraceus*, which are unknown, might ultimately affect adult color patterns. In lobsters, for example, juvenile diet has been shown to affect color patterns through both genetically determined and phenotypically plastic pathways (Tlusty and Hyland 2005).

Hypothetically, *P. ochraceus* could change color ontogenetically, a phenomenon that occurs in other taxa (Booth 1990). Although direct observations of color change have not been made, support for ontogenetic color change in *P. ochraceus* comes from frequent observations of intermediate-size orange sea stars with purple arm tips (Figure 4), and observations of orange stars regenerating a mostly purple arm bud. Ontogenetic color change in limited parts of an organism's body has been observed in other marine invertebrates (e.g., Tlusty and Hyland 2005). The delayed onset of orange coloration may be related to the cryptic coloration afforded to very small (<30 mm), nonorange-colored sea stars on coralline algae in our study range, where they are often found as newly settled recruits. This is analogous to *Cancer irroratus* rock crabs, where coloration is conspicuous in adults but cryptic in newly settled juveniles (Palma and Steneck 2001). Moreover, other investigators (E. Sanford, pers. comm. 2006) and we ourselves have noted that most small (e.g., <30 mm) sea stars tend to be grayish purple or grayish brown along the exposed Pacific coast, indicating that adult purple and brown stars also change color but perhaps not as dramatically as orange adults. Apparently, a different pattern is seen in some habitats in the northeastern Pacific where small sea stars are more commonly orange, a color that is more cryptic on their preferred settlement habitat there (R. Paine, pers. comm.), but extensive observations of color ratios at different sizes have not been made for those populations.

Differences with Protected-Water Populations

The frequencies of color morphs in *P. ochraceus* populations from protected waters in the northeastern Pacific are in stark contrast to those we observed for open-coast populations, which might shed light into the mechanisms underlying color polymorphism in this species. First, protected-water populations are much more variable in color ratios, and individual sites tend to be dominated by one color morph or another. For example, on San Juan Island (48.5° N, 123° W), purple stars dominate. Of 250 individuals sampled at six sites on San Juan Island by R.D.S. in September 2005, only 4.8% were orange. Likewise, purple individuals dominate populations in Georgia Strait (D. Eernisse, pers. obs.) (Harley et al. in press) and at sites along the Inside Passage of southeastern Alaska (C. Baxter, pers. obs.). Yet, on Orcas Island, adjacent to San Juan Island, populations are dominated by orange individuals (R. Strathmann, pers. obs.). In addition, the purple stars in these protected-water populations are far more vivid than their open-coast counterparts, although small numbers of brightly colored purple stars have been observed at open-coast sites (E. Sanford, pers. comm.). At protected sites, orange individuals are much paler in color, and the brown color morph seen on the open coast is largely absent (RDS, pers. obs.).

Wave exposure, water chemistry, and available food resources differ substantially between protected and outer-coast sites. Local differences in wave exposure might become manifest through differences in larval settlement patterns. In the embayments of Puget Sound and other protected waters, founder effects might dominate so that infrequent settlement events skewed by chance toward one color morph or another could result in similarly skewed adult sea star populations. This hypothesis is supported by data on the size structures of *P. ochraceus* populations at six San Juan Island sites, which showed that sea stars <70-mm radius were absent from 250 sampled individuals compared with 27% of all observations for the open coast. This finding suggests that recruitment events are more episodic in these protected waters. Salinity and pH are likely to be different in protected waters compared with open-coast sites, but at present we do not know the effects of water chemistry on sea star pigmentation. *Pisaster ochraceus* populations in quiet water environments also likely differ from open-coast populations in diet, because *Mytilus californianus*, a prominent bed-forming space occupier on much of the open Pacific coast, is not found in great densities on San Juan Island or at other protected-water sites. Differences in diet could hypothetically result in different color ratios and different color tones in open- versus protected-water populations, but dietary differences do not explain how polymorphism is maintained with such consistency across the broad geographic range represented by our outer-coast study sites. Moreover, observations from protected-water populations must be taken with caution because it has been suggested (Ricketts et al. 1985) that these populations are a subspecies of *P. ochraceus* (i.e., *P. ochraceus confertus*).

CONCLUSIONS AND FUTURE DIRECTIONS

In 1959, Feder lamented, “Although the starfish *Pisaster ochraceus* is one of the most conspicuous animals to be found along the rocky shores of the Pacific Coast … its natural history is poorly known” (Feder 1959:721). Nearly 50 yr later, because of Feder and others, knowledge of the natural history of *P. ochraceus* has increased, but causes of a most obvious characteristic—its striking color polymorphism—remains a mystery.

Several of the key questions raised by our observations can become the focus of a renewed effort to understand patterns of color in *P. ochraceus*. Elucidation of the gene(s) and pigment complexes responsible for color is a fundamental gap in our understanding of color patterns. Mating experiments involving crosses of variously colored parents might help determine the inheritance patterns of color, although typically high mortality in laboratory cultures may confound interpretation of results. Basic biological questions need to be assessed in an ecological context, considering how variation in diet, water chemistry, and biological interactions can affect pigmentation and the occurrence and mechanisms of color change. Moreover, understanding the extent to which larval dispersal effectively mixes populations will provide insight into the role that genetic drift could play in skewing color ratios. Clarification of population genetic structure and phylogeographic patterns will help to address the question of whether protected-water populations are genetically distinct from one another and from open-water populations. Although addressing these questions will be a challenge, improved understanding of the mechanisms of color variation in this common sea star would be greatly appreciated by the many amateur naturalists and professional biologists who have been intrigued by this conspicuous tide-pool animal.

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Spatial patterns in recruitment and growth of the mussel *Mytilus californianus* (Conrad) in southern and northern California, USA, two regions with differing oceanographic conditions

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ABSTRACT

Mussels, *Mytilus californianus*, and other benthic invertebrate populations on the wave-exposed intertidal coast of the eastern North Pacific are impacted by a suite of biotic and abiotic factors on both local and larger geographic scales. Previous surveys of mussel abundances along the California coast have revealed that mussels, in general, are very abundant in northern California while low in southern California. Nevertheless, mussel abundances in southern California are highly variability with a small number of sites that are characterized as having moderately high to high abundances. To elucidate driving factors of mussel abundances in these regions, we investigated recruitment and growth rates of mussels in 1) northern and southern California, two regions separated by ca. 900 km and exposed to vastly different oceanographic processes and 2) within southern California at sites with moderately high mussel abundances and at sites with low abundances. We found that recruitment and, to a degree, growth may be important factors driving variable abundances of mussels within southern California but could not explain patterns along the entire California coast. Recruitment and growth rates were low in northern California even though mussels were highly abundant. Conversely, recruitment and growth in southern California were significantly higher than northern California and, within the region, were higher in sites characterized by moderately high abundances. Among regions, differences in recruitment and growth are likely driven by large scale oceanographic patterns such as upwelling affecting larval transport and temperature affecting growth. Within southern California, local oceanographic processes likely enhanced or inhibited recruitment or growth leading to differences in measures between closely located sites.

1. Introduction

Macroinvertebrate communities in rocky intertidal habitats are influenced by benthic processes, such as competition and predation, and physical disturbance, such as that from wave activity, which can drive patterns of abundances of adult populations (e.g. Connell, 1961; Paine, 1966; Dayton, 1971). Equally important are oceanographic conditions that, for example, can carry larvae on- or offshore (e.g. Roughgarden et al., 1988) or supply coastal communities with nutrients for primary productivity or food for benthic filter feeders (e.g. Menge et al., 1997, 1999, 2003; Blanchette et al., 2002, 2006). For example, adult barnacle abundances differ greatly along the eastern North Pacific coast, with high barnacle cover in Oregon and low cover in the northern and central portions of California, that are suggested to be linked to the frequency of upwelling and relaxation events leading to differing levels of larval supply (Roughgarden et al., 1988; Connolly and Roughgarden, 1998). Furthermore, oceanographic conditions bringing phytoplankton nearshore can drive rocky intertidal communities towards those dominated by filter feeders as opposed to macrophyte dominated communities where plankton supply is low (Menge et al., 1997).

Along the eastern north Pacific coast, the mid rocky intertidal zones on wave-exposed shorelines are dominated by mussels, mostly *Mytilus californianus* Condrad (Ricketts et al., 1968). Mussels congregate in large clumps that can be several layers thick forming a mussel bed that can provide space and shelter for a large number of associated species. In addition, as filter feeders that consume large amounts of plankton and detritus, they function as an energy link between pelagic and benthic systems providing secondary production for a wide number of predators. A survey of mussel abundances along three regions of the California coast (southern, central, and northern) reveals high variability among regions (particularly between southern and northern California) as well as among sites within a region (Smith,

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2005). In general, mussel abundances are relatively low throughout the Southern California Bight (SCB), including both the mainland and offshore islands, and central California but are much more abundant in northern California (Monterey Bay and north). Despite this regional trend, there are numerous locations in the SCB that are characterized with moderate to high mussel abundances. The driving forces behind these patterns are unknown and likely attributed to multiple factors. Here, we explore patterns of recruitment and growth within and between southern and northern California, two regions with differing oceanographic conditions, to elucidate whether these variables are linked to adult mussel abundances.

Mussel abundances can be driven by numerous biotic and abiotic factors on both local and large geographic scales. On a local scale, mussels are affected, for example, by sea star predators that can control abundances as well as the distribution of mussels into the low intertidal zone (Paine, 1966, 1974). Desiccation and submergence time, or the amount of time available for feeding, also have been shown be important driving forces in mussel abundances and distributions (Dehnel, 1956; Harger, 1970; Behrens Yamada and Dunham, 1989; Harley and Helmuth, 2003).

Mesoscale (100s of km) oceanographic conditions are also an important driving force for adult mussel populations. Supply of food and mussel larvae varies greatly depending on numerous oceanographic patterns, most notably upwelling and relaxation events (Farrell et al., 1991; Roughgarden et al., 1991; Miller and Emlet, 1997). Because meroplanktonic larvae and other planktonic organisms are carried by currents, recruitment and food supply patterns are heavily influenced by movement of coastal water masses on- or offshore (Farrell et al., 1991; Roughgarden et al., 1991, 1994; Gaines and Bertness, 1992; Shanks et al., 2000; McCulloch and Shanks, 2003). During periods of upwelling, plankton travel with water masses moving offshore and accumulate at offshore frontal boundaries where cold and saline upwelled water meets warmer and less saline water (Roughgarden et al., 1994). This convergence zone can move, depending on the winds, and can transport larvae or planktonic food onshore during periods of relaxed upwelling (Farrell et al., 1991; Roughgarden et al., 1991; Miller and Emlet, 1997).

The supply of larvae can have important implications in rocky intertidal community structure (e.g. Underwood et al., 1983; Gaines and Roughgarden, 1985; Connolly and Roughgarden, 1998; Connolly et al., 2001). When larval supply is limited, the importance of benthic processes is much reduced and adult macroinvertebrate abundances are driven more by recruitment rates (Underwood et al., 1983; Gaines and Roughgarden, 1985; Ebert and Russell, 1988; Roughgarden et al., 1988; Farrell et al., 1991; Connolly et al., 2001). Furthermore, low larval supply driven by coastal upwelling dynamics can influence community composition by enhancing conditions whereby macroalgae dominate space (Schiel, 2004). When larval supply is not limited, benthic interactions, such as competition and predation, are more intense (Gaines and Roughgarden, 1985; Connolly and Roughgarden, 1998; Connolly et al., 2001).

Besides larval supply and recruitment, post-settlement processes such as growth rates also can be important in structuring adult populations of macroinvertebrates (Gaines and Roughgarden, 1985; Bertness et al., 1991; Connolly and Roughgarden, 1998; Blanchette et al., 2007). Variable growth rates may affect community structure and population interactions (Bertness et al., 1991), and, in turn, adult populations through alterations of susceptibility to physical stress (Vermeij, 1971), predation (Paine, 1976; Robles et al., 1990), and competition (Buss, 1986) and availability of free space (Gaines and Roughgarden, 1985). In addition, growth rates impact the reproductive potential of the population as reproductive output increases exponentially with size (Kautsky, 1982). Oceanographic regimes, mostly temperature but also supply of food, can greatly influence growth rates along local (among sites) and larger geographic scales (among regions).

Recently, there have been a number of studies attempting to elucidate the importance of larger scale oceanographic conditions on mussel distributions (Broitman et al., 2005; Phillips, 2005; Blanchette et al., 2006, 2007; Blanchette and Gaines, 2007). On Santa Cruz Island, one of the southern California offshore Channel Islands (see Fig. 1), the western side of the island experienced cold temperatures, a higher frequency of upwelling, and low recruitment rates as compared to opposite patterns on the eastern side (Broitman et al., 2005). Recruitment rates, abundances, and growth of mussels in this region were positively associated with sea surface temperatures. Food availability, as indicated by chl-*a* concentrations, were not related (Blanchette et al., 2006). Additional studies have compared mussel populations in the immediate area surrounding Point Conception, a biogeographic break separating colder central California waters from warmer southern California waters (see Fig. 1). Here, warmer southern California waters with higher mussel abundances were found to have higher growth rates that were related to temperature and wave exposure but, again, were not correlated with food availability (Phillips, 2005; Blanchette et al., 2007). Abundances north and south of Point Conception were not driven by differential recruitment as recruitment was low in the entire region (Blanchette and Gaines, 2007).

Despite numerous reports on oceanographic conditions and their influence on mussel community dynamics, gaps in our knowledge still exist. Much of the previously published work has concentrated on areas immediately surrounding Point Conception in the northern portion of the SCB by Santa Barbara and central California. Little work has been conducted in the other portions of southern California (i.e.. Los Angeles and San Diego; see Fig. 1). In addition, few comparisons have been conducted on recruitment and growth between the SCB and northern California. The purpose of this study was to compare recruitment and growth of mussels in two regions, southern and northern California, subjected to different oceanographic patterns and characterized by differing adult abundances. Recruitment and growth of mussels were measured at several sites in southern and northern California to determine geographic differences between the two regions and at sites within southern California with differing adult mussel characteristics to determine if there is a relationship with adult mussel populations.

2. Methods

2.1. Site Selection

Nine sites were selected in two non-adjacent regions, northern and southern California, separated by ca. 900 km of coastline (Fig. 1). The SCB is characterized as a transition zone between temperate and subtropical regimes with sea surface temperatures ranging yearly from ~11 to 23 °C. Upwelling events in the region are infrequent and often only occur in short time periods during the spring season (Littler, 1980; Hickey, 1993). Much of the southern California mainland coastline is protected from large swell events because of the orientation of the coast and the presence of the Channel Islands that act as a barrier to long-distance swell events. Northern California is subjected to much colder waters ranging yearly from ~8 to 17 °C. Upwelling in northern California is more intense and longer with few relaxation events (Bakun and Nelson, 1991). Locations along the northern California coastline are also seasonally exposed to large swell events.

Of the nine sites selected, six sites were located in the SCB and three sites in northern California. Six sites were chosen within southern California, a region with variable mussel abundances, with three locations considered to have moderate to high mussel abundances and thick beds and three with low abundances and thin beds. In northern California, a region characterized by consistently high mussel abundances and very thick beds, only three locations were chosen. The scale of mussel abundances (high to low) was based on measures of mussel bed thickness at each of the locations. Bed

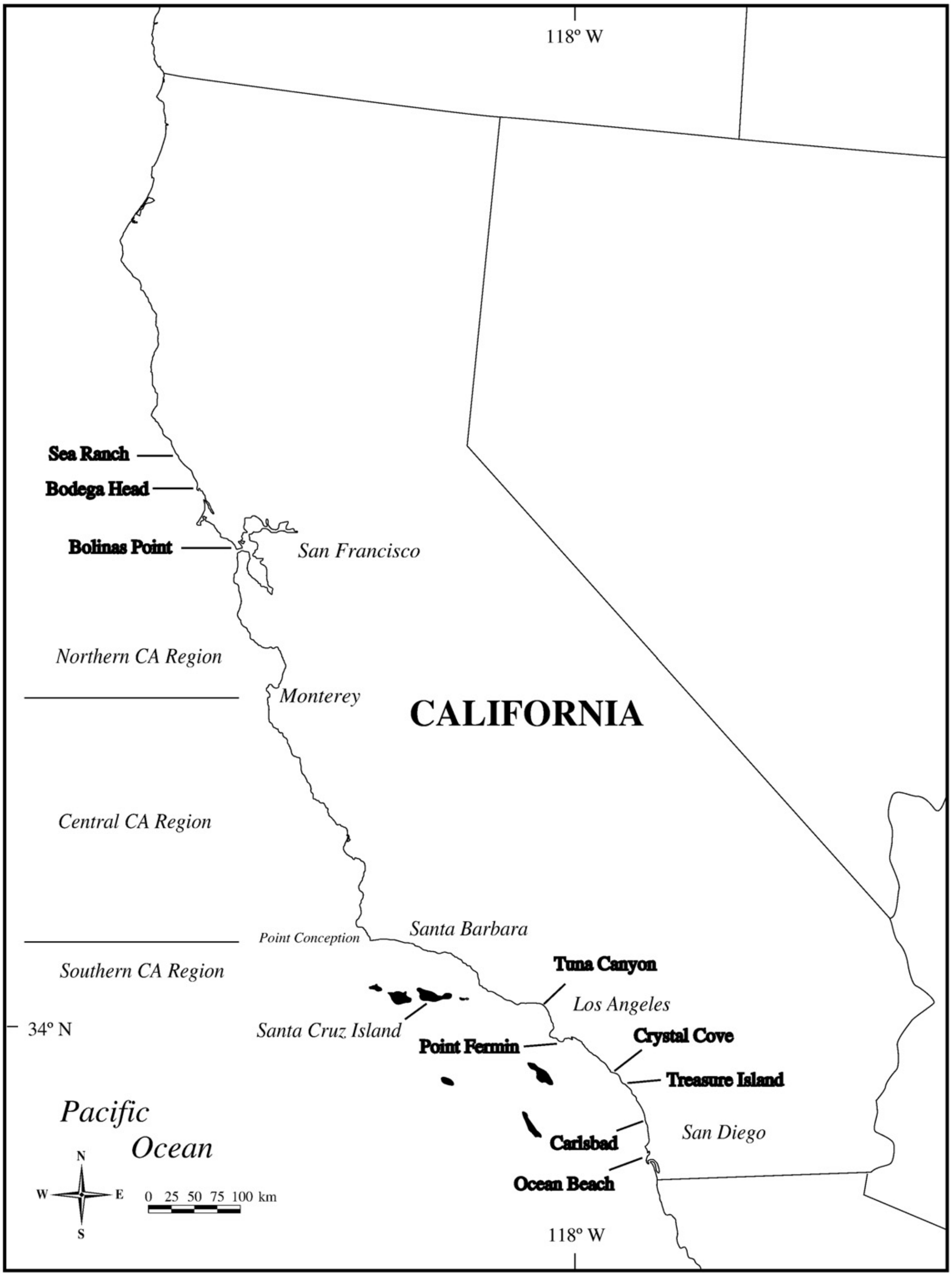

Fig. 1. Map of nine sampled sites along the wave-exposed coast of California. Also indicated are the three regions of California: southern CA separated from central CA at Point Conception and northern CA separated from central CA at Monterey.

thickness was measured at twenty random points in five 0.5×0.7 m quadrats randomly placed within the middle of established mussel beds for a total of 100 points. At each of these points, a steel pin was pushed through the bed until it reached the understory rock and the length measured. Mussel bed thickness was used as a proxy for mussel abundances as it was found to be steeply and positively related with biomass ($R^2=0.92$, $p<0.001$) and adult density ($R^2=0.54$, $p<0.001$; Smith, 2005). The areal extents of the mussel beds were not measured but are not likely good comparisons of mussel abundances across regions or sites as mussel bed size depends on the slope and size of the intertidal zone which can be highly variable among locations and between regions. Instead, measures of mussel abundances within established beds were used as considered by others (Blanchette and Gaines, 2007). The three SCB sites considered to have low mussel abundances were characterized with thin, single layered beds measuring 40.9±2.7 (mean±SE) mm deep while the three sites considered to have moderate/high mussel abundances were relatively thick and multi-layered reaching 95.4±10.7 mm in depth (site specific measures in Table 1). The northern California sites were characterized by very thick mussel beds (145.5 ± 10.9 mm; Table 1).

2.2. Recruitment

At each site, 6 or 7 recruitment collectors (Tuffy brand pot scrubbers) were bolted to the rock within mussel beds and replaced every month for 1 year starting March 2003. Tuffies were placed in the middle of mussel beds to standardize effective tidal heights among sites, since mussel bed tidal height ranges may vary due to facing slope, wave action, and other oceanographic or geologic factors. Tuffy scrubbers have been commonly used for mussel recruitment measures (e.g. Menge, 1992; Phillips and Gaines, 2002) as they simulate the physical structure of filamentous algae and byssal threads in which mussel larvae normally settle (Petersen, 1984). Collected Tuffies were returned to the lab and frozen until further analysis.

Recruitment collectors were processed by thawing the Tuffy, rinsing with fresh water, and collecting all solid materials in a 250 µm sieve. Recruits were counted under a dissecting microscope. In many cases, only 3 or 4 collectors were processed per month, as variation within a month at a site was small. In a few cases, collectors were lost, possibly due to wave activity or human intervention, reducing the sample size to two collectors at sites in certain months. The mean number of recruits per collector per month was calculated for each site. Although *Mytilus* recruits were not identified to species, observations of newly recruited mussels into open patches and subsequent aging to juvenile and adult mussels suggested that only *Mytilus californianus* were recruiting to the sites. The bay mussel *Mytilus galloprovincialis* Lamarck, a less common species on the open coast, has been observed to exhibit episodic recruitment to the wave-exposed rocky intertidal zone (Smith per. obs.) but are easily distinguishable as juveniles. During this study, *M. galloprovincialis* were not seen in mussel cohorts observed throughout the year-long experiment and were rare in harvested samples of already established adult mussel populations (Smith, 2005). Furthermore, previous studies on mussel recruitment have found that more than 90% of collected recruits are *Mytilus californianus* (see Blanchette and Gaines, 2007).

2.3. Growth

At each site, 80 mussels of a range of sizes (25–80 mm, but mostly within 40–60 mm range) were haphazardly chosen and tagged in March of 2003. Tagged mussels were located in the middle of mussel beds to standardize effective tidal heights. Numbered wire tags were superglued to the surface of mussels and each mussel mapped using a grid system. For ease of sampling and to limit damage of the mussel bed through manual movement of mussels and weakening of their attachment strengths, only mussels on the upper surface of the bed were marked. Although measuring growth of surface mussels may bias results by monitoring mussels that likely exhibit the highest growth, similar methods were used at all sites to ensure comparability. The entire length of the mussel was measured initially. An etch mark was then made near the posterior shell edge of each mussel, and the length from the etch mark to the posterior lip of the mussel was measured. Similar methods of marking mussels have been used in other growth studies (Seed, 1976; Behrens Yamada and Peters, 1988; Behrens Yamada and Dunham, 1989; McQuaid and Lindsay, 2000; Steffani and Branch, 2003; Blanchette et al., 2007). Every three to four months for 1 year, the etch mark to the lip was re-measured to monitor growth and standardized to growth per month (30 days).

Table 1
Site name, abbreviation, county, and location (latitude and longitude)

Site	Site code	County	Location		Bed thickness (mm)
Southern California					
Ocean Beach	OCB	San Diego	32° 44′ 38″	117° 15′ 19″	35.8 (4.0)
Carlsbad	CBD	San Diego	33° 06′ 45″	117° 20′ 41″	88.0 (8.6)
Treasure Island	TRE	Orange	33° 30′ 48″	117° 45′ 33″	42.2 (3.9)
Crystal Cove	CRC	Orange	33° 34′ 13″	117° 50′ 15″	106.8 (8.2)
Point Fermin	PTF	Los Angeles	33° 42′ 26″	118° 17′ 09″	44.8 (1.8)
Tuna Canyon	TUN	Los Angeles	34° 02′ 20″	118° 41′ 17″	91.4 (15.5)
Northern California					
Bolinas	BOL	Marin	37° 54′ 13″	122° 43′ 34″	125.8 (7.4)
Bodega Head	BOD	Sonoma	38° 18′ 58″	123° 04′ 19″	163.5 (13.9)
Sea Ranch	SEA	Sonoma	38° 43′ 48″	123° 29′ 18″	147.3 (12.2)

Also reported is mean site bed thickness (±SE) for all nine sites (Smith, 2005).

Because a portion of the mussels or tags were periodically lost, new mussels were tagged and measured approximately every three to four months during resampling periods in order to maintain a sufficient sample size. Despite loss of tags, data were not compromised as we examined growth rates for the site population for each season; we did not attempt to measure growth for the populations at each site over a year period. Monthly mussel growth was calculated for four seasons throughout the year-long study. Although we attempted to use the same range of initial sizes of mussels, the size frequency of tagged individuals varied at sites depending on the population size frequency. In addition, the size frequency of tagged mussels also varied seasonally due to lost tags and several remarking sampling efforts. For presentation purposes, all data are included in the figures. However, to account for variability in the number of replicates in the small and large size classes, we truncated our data to include only those individuals with an initial length between 40 and 60 mm.

2.4. Analysis

Recruitment and growth data were analyzed using the Minitab statistical program (version 13.0). Data were tested for normality and homogeneity of variance and transformed when necessary. To test for spatial differences in recruitment, a Nested Two Factor ANOVA was performed with region (southern v northern California) and month as fixed factors and sites nested within regions. The mean number of mussel recruits collector^{-1} month^{-1} (log transformed) was calculated for twelve months at all sites in southern California and compared with sites in northern California. To determine if recruitment varied among beds in southern California with differing adult mussel populations, we calculated the mean number of mussel recruits collector^{-1} month^{-1} for twelve months at sites with mussel populations characterized by thick beds and compared them with recruitment at sites with thin beds. Log transformed data were analyzed using a Nested Two Factor ANOVA with bed thickness type (thick v thin) and month as factors and sites nested within bed thickness type.

Growth data for each individual were converted to growth (mm) per 30 day month (mm) and tested for normality and homogeneity of variance. To test for regional differences in growth, a Nested Two Factor ANCOVA was used on untransformed data with region and season as fixed factors, sites nested within regions, and initial size as a co-variate. To determine if growth varied among locations in southern California with differing adult populations, untransformed growth data were analyzed using a Nested Two Factor ANCOVA with bed thickness type and season as fixed factors, sites nested within bed thickness type, and initial size as a covariate. In order to present the large data set in a clear manner, several graphs were constructed indicating the regression line of growth per month plotted against initial size. Three graphs were constructed showing: 1) each site individually across all seasons, 2) combined southern and northern California sites for each of the four seasons, and 3) combined locations within southern California with thick beds/high mussel abundances and locations with thin beds/low abundances for each of the four seasons.

We attempted to construct von Bertalanffy growth curves and compare these slopes to determine differences among sites. However, growth at some sites was practically absent and, with a small degree of measuring error, some individuals exhibited negative growth. In addition, because growth was extremely low, faster rates of growth in small mussels as compared to large mussels at some sites could not be detected. Due to these issues, growth curves could not be satisfactorily constructed.

3. Results

3.1. Recruitment

The mean number of recruits per artificial collector over the year sampling period was highest at Carlsbad and Tuna Canyon in the SCB and was lowest at Bolinas and Sea Ranch in northern California (Fig. 2). The largest number of recruits found in one collector throughout the study was ~1550 recruits at Carlsbad in August. Sites in northern California had consistently low recruitment while southern California sites were highly variable. Averaging sites within a region revealed very low monthly recruitment rates in northern California while recruitment rates in the SCB were an order of magnitude higher (Fig. 2). A Nested Two Factor ANOVA revealed significant differences between regions and among sites nested in regions while a temporal trend was not detected. A significant interaction between region and month was found (Table 2) with weak patterns of temporal differences in some locations in the SCB, mostly driven by high rates of recruitment at Carlsbad in late summer/early fall.

Within the SCB, two of the three sites with thick beds/high adult abundances had much higher recruitment rates than the three sites with thin beds/low adult abundances (Fig. 2). Here, only 9.4±1.3 (mean±SE) recruits per month per collector were counted in thin beds as opposed to 79.1±13.7 recruits per month per collector in thick beds. In southern California, recruitment rates were significantly higher in the sites with thick beds than those sites with thin beds with significant differences also found among sites nested within thick or thin beds (Nested Two-Factor ANOVA, Table 2); temporal differences and an interaction effect were not detected.

Table 2
Summary of statistical results for Two Factor ANOVAs on recruitment and Two Factor ANCOVA on growth data

Data	Factor	*df*	MS	*F*	*p* value
Recruitment	Region	1	26.10	59.7	<**0.001**
	Month	1	0.361	1.3	0.250
	Region × Month	1	1.68	6.2	**0.013**
	Site (region)	7	16.20	59.7	<**0.001**
	Thickness	1	7.46	34.7	<**0.001**
	Month	1	0.38	1.8	0.183
	Thickness × Month	1	0.72	3.3	0.069
	Site (thickness)	4	9.68	45.0	<**0.001**
Growth	Initial size (covariate)	1	4.99	5.43	**0.020**
	Region	1	11.12	12.2	**0.001**
	Season	1	4.76	5.2	**0.023**
	Region × Season	1	10.19	11.1	**0.001**
	Site (region)	7	11.59	12.6	**0.001**
	Initial size (covariate)	1	7.87	5.0	**0.015**
	Thickness	1	2.39	1.8	0.178
	Season	1	0.82	0.6	0.430
	Thickness × Season	1	0.76	0.6	0.446
	Site (thickness)	4	6.88	5.3	<**0.001**

Reported are degrees of freedom (*df*), mean squares (MS), *F* stat, and *p* values for each of the analyzed factors. Significant *p*-values are indicated in bold.

3.2. Growth

Growth rates were low and ranged from almost no growth to ~3 mm month^{-1} depending on the site and initial size of the individual (Fig. 3a). Overall, mussels at Tuna Canyon grew the fastest; the exception was small mussels at Point Fermin, which grew slightly faster but with the rate of growth slowing markedly with larger individuals. The lowest growth occurred at the three northern California sites. Most sites in southern California exhibited slightly negative growth slopes with increasing size except Point Fermin, which exhibited a much steeper negative slope. In northern California, slopes varied among sites but were relatively flat due to low growth overall. Between regions, growth was significantly higher in the SCB than in northern California with significant differences among sites nested within regions (Fig. 3a,b; Nested Two Factor ANCOVA, Table 2). In addition, growth rates differed significantly among seasons (Table 2) with relatively high growth in summer and spring for both regions and lowest growth in winter (Fig. 3b). In fall, growth rates

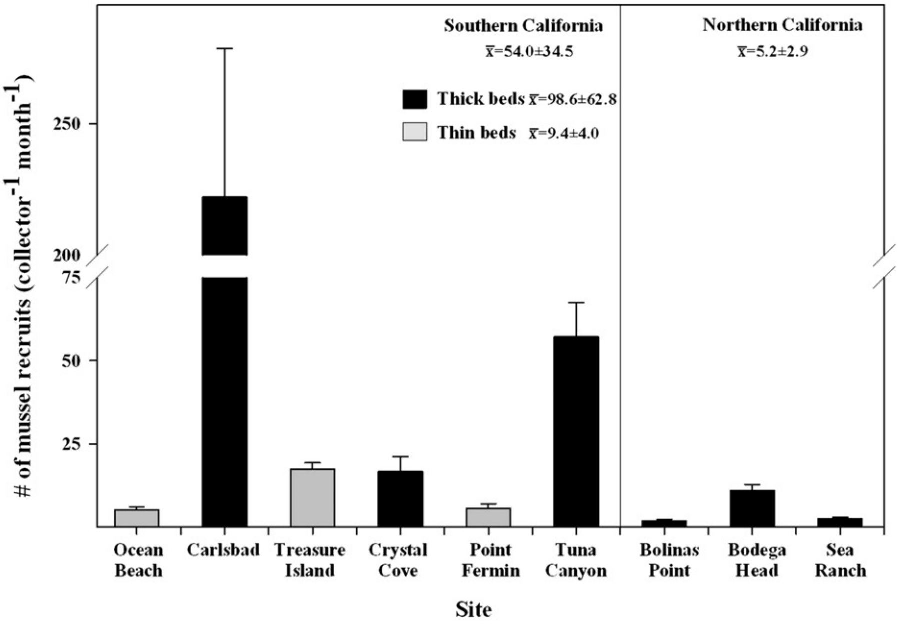

Fig. 2. Mean number of mussel recruits per collector per month (±SE) for six southern California sites and three northern California sites. In southern California, sites with thick mussel beds (high abundance) are noted by black bars while gray bars note sites with thin beds. All sites within northern California had thick beds. Mean recruitment rates (±SE) are noted for the southern and northern California regions and for thick and thin beds within southern California.

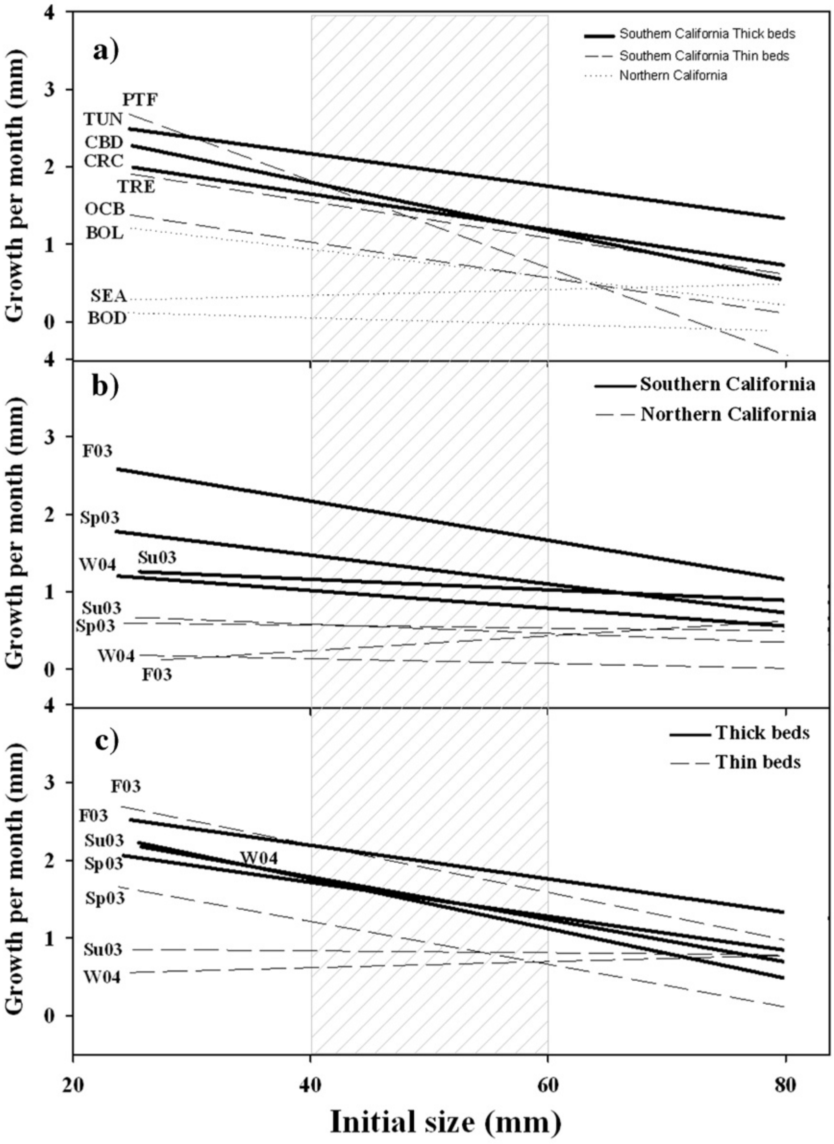

Fig. 3. Slope of growth of marked mussels (mm per month) versus initial size (mm) for a) all nine sites sampled combining all seasons, b) southern California sites combined and northern California sites combined during the four sampled seasons (F03 = Fall 2003; SU03 = Summer 2003; SP03 = Spring 2003; and W04 = Winter 2004), and c) southern California sites with locations characterized by thick mussel beds (= high mussel abundance) combined and thin mussel beds (= low mussel abundance) combined during the four sampled seasons. Site abbreviations are located in Table 1. Length of slopes are artificially extended or cut-off at 80 mm. The shaded region indicates the size class that was used for statistical analyses (see Methods).

across all sizes were higher than any other season in southern California. In northern California, there was a positive slope causing a significant interaction between region and season (Table 2).

Within the SCB, overall growth was generally higher in the three locations characterized with thick beds than locations with thin beds (Fig. 3a,c). Sites nested within bed thickness were found to be significantly variable but no difference was found between the thin and thick beds (Nested Two Factor ANCOVA, Table 2). In fall, growth ranked the highest for both bed types with a pattern of small to medium sized mussels growing faster in thin beds than thick beds (Fig. 3c). In thick beds, there were little differences in growth or slopes among seasons. In thin beds, however, growth rates and growth slopes varied with season: in summer and winter, growth slopes were flat or slightly positive while slopes in fall and spring were negative. Growth among seasons, however, was not found to differ significantly nor was an interaction found between bed type and season (Table 2).

4. Discussion

Recruitment and growth were important factors affecting the distribution of mussels within the southern California Bight (SCB) but could not explain patterns along the entire California coast. Higher recruitment and growth in mussel populations in the SCB characterized by low to moderately high adult abundances were contrasted with low recruitment and growth in northern California, a region with markedly higher adult abundances. Within the SCB, recruitment and growth were related to the level of adult abundances as locations with thick beds (higher adult mussel abundances) had higher recruitment and growth rates than locations with thin beds (lower abundances). Geographic trends in recruitment and growth across a large geographic scale that differ oceanographically suggest that different processes affected mussel populations within the two regions.

4.1. Recruitment

Larval transport and recruitment are known to be heavily influenced by oceanographic processes. Coastal circulation promotes transport of larvae to the shore in some areas, such as Oregon, while in other areas, such as northern and central California, frequent upwelling events transport larvae offshore (Roughgarden et al., 1988, Connolly and Roughgarden, 1998). Recruitment at sites in northern California was consistent with patterns produced by strong upwelling and offshore transport of larvae. Results suggest, in accordance with other studies (e.g. Broitman et al., 2005, 2008), that mussels are potentially limited where upwelling is frequent. In the SCB, however, upwelling is generally weak and sporadic (Hickey, 1993). The oceanographic regime in the SCB may be facilitating larval transport and higher recruitment to rocky intertidal habitats in the region. Ebert et al. (1994) reported higher recruitment of urchins in southern California compared to northern California and suggested that the pattern was likely due to greater retention of water in the SCB.

Recruitment rates of *Mytilus* at many of our southern California locations were similarly low to other locations in the region (Blanchette and Gaines, 2007; Broitman et al., 2008). These locations, although with higher recruitment rates than northern California, were several magnitudes lower than observed in Oregon, a region with intermittent upwelling (Broitman et al., 2008). However, contrasting other SCB recruitment studies, we found two locations in the central portion of the bight where recruitment was relatively high. On occasion, recruitment rates at Carlsbad were extremely high with levels similar to that of Oregon. This high variability in the region denotes the need for long term recruitment monitoring studies to include more location into the southern and central portions of the SCB.

The factors leading to high recruitment at some sites within the SCB need to be further investigated. It is unlikely that the adult population is regulating the number of recruits through local recruitment from the resident population, as *Mytilus californianus* has exhibited no difference in large-scale proportions of genetic types, suggesting that gene flow occurs along the coastline and that mussel larvae disperse long distances (Engel, 2004). Alternatively, very nearshore oceanographic processes at each of the sites may explain differences in recruitment rates. Several processes on a local level may affect larval supply including internal waves, surface slicks and foam lines, and Langmuir flow (Shanks, 1983, 1995; Kingsford and Choat, 1986; Shanks and Wright, 1987; Kingsford, 1990; Kingsford et al., 1991; McCulloch and Shanks, 2003; Shanks et al., 2003). For example, at sites with low recruitment, local currents may transport incoming larvae seaward or topographically generated fronts may act as a barrier to larvae reaching the shore (McCulloch and Shanks, 2003). Similarly, local currents or topography may facilitate high recruitment by transporting larvae inshore. Several studies (Shanks, 1983, 1986; Kingsford and Choat, 1986; Kingsford et al., 1991) have reported that some larvae of coastal invertebrates and fishes are transported shoreward in surface slicks generated over tidally forced internal waves. Some meroplanktonic larvae can also behaviorally utilize vertically sheared flows to aid shoreward progression (Garland et al., 2002). For example, offshore larvae from benthic populations can be carried toward the coast during periods of upwelling as bottom water flows towards the shoreline (Garland et al., 2002). Other invertebrate larvae may be retained between the shore and an upwelling front due to diel vertical migrations (Poulin et al., 2002). Understanding local variations in recruitment of invertebrates with broadly dispersing larvae and the processes affecting these variations can aid in understanding how to manage and conserve at-risk populations. This is especially important for mussels in southern California where populations have declined over the past few decades (Smith et al., 2006).

Without knowledge of specific local oceanography at our sites, it is difficult to ascertain reason for differing recruitment rates. Recruitment rates differed greatly at sites in close proximity (i.e.., Tuna Canyon and Point Fermin) with no obvious geomorphological differences that could affect oceanographic patterns. However, it is interesting to note that Carlsbad, the site with highest recruitment, is located near the mouth of Agua Hedionda Lagoon. Here, local oceanography may be influenced by the lagoon and may result in larval transport onshore. Studies investigating river plume and estuarine front dynamics suggest that buoyant coastal discharges may induce coastal currents locally, causing a frontal circulation at the mouth that acts as a barrier to larvae dispersal (Kingsford and Suther, 1994; Vargas et al., 2006). Here, accumulation of larvae at the front edge may facilitate transport to some locations nearby (Eggleston et al., 1998; Vargas et al., 2006) as the plume circles back around near the coastline. Although flow out of Agua Hedionda is likely low, a front may occur near the mouth where mussel larvae may accumulate and then be transported back to shore during relaxation of estuarine driven fronts (Eggleston et al., 1998) or when strong tidal movements move the front shoreward.

It is clear from other work (Broitman et al., 2008) that there is some level of year-to-year variation in recruitment rates possibly due to temporal variation in upwelling frequency and longevity. Our study monitored recruitment over a year period and thus did not detect longer term temporal change. Nonetheless, the regional patterns we detected are unlikely to change over time as geographic recruitment patterns appear consistent over multiple years (Broitman et al., 2008). Here, above and below normal levels of recruitment during certain years of recruitment monitoring along the eastern north Pacific coast appeared consistent among regions.

4.2. Growth

Growth of mussels, like recruitment, showed geographical variations with southern California exhibiting higher growth than northern California. Geographical differences in growth rates likely reflect differences in temperature between the two regions. Phillips (2005) and Blanchette et al. (2007) suggested that observed differences in growth between sites north and south of Point Conception were likely attributable to temperature differences. Within southern California, growth rates of mussels and barnacles were found to be positively correlated with SST (Blanchette et al., 2006) when comparing growth at sites on a southern California offshore Channel Island subjected to a persistent thermal gradient on opposite sides of the island. Mussels are known to grow rapidly in temperature between 15 and 19 °C, with decreases in growth observed in temperatures above and below that range (Coe and Fox, 1942, 1944). At the southern California sites, mean annual temperatures (1995–2003; Advanced Very High Resolution Radiometer) among sites ranged from 16 to 17 °C, within the range of highest mussel growth, while yearly mean temperatures at our northern sites were approximately 12 °C, well below the range of optimal growth.

Food availability can also be a factor influencing mussel growth as filter feeders are known to exhibit higher growth in areas with higher food availability (e.g. Duggins et al., 1989; Bertness et al., 1991; Dahlhoff and Menge, 1996; Menge et al., 1997; Sanford and Menge, 2001). However, recent work has suggested that other factors may be determining growth rates, either separately or in conjunction with productivity (Sanford and Menge, 2001; Phillips, 2005; Blanchette et al., 2006). Numerous studies have reported that growth of mussels and other filter feeders north and south of Point Conception was not explained by food availability or food quality (Phillips, 2005; Blanchette et al., 2006, 2007). They suggested that temperature likely played a more significant role in determining growth. Measures of food availability were beyond the scope of this study thus we cannot expand on the effects on growth at our sites.

Unlike regional differences, variation in growth in southern California could not be attributed to temperature, since all sites within the SCB fell within the temperature range of highest growth (Coe and Fox, 1942, 1944). Furthermore, sites with low growth were in close proximity (<50 km) to sites with high growth and thus had very similar seawater temperatures. Although Blanchette et al. (2006) attributed differences in growth between locations in close proximity within southern California to temperature, they conducted work on an offshore island subjected to quite different thermal regimes on opposite sides of the island.

Alternative to temperature causing variability in growth rates within southern California, potential factors such as food availability and wave activity may be important local factors/drivers. First, although cholorophyll a, an indicator of food availability, was consistently low throughout the SCB using satellite data from large areas (40×50 km — meridional×zonal; Smith, 2005 also supported by nearshore measurements by Blanchette et al., 2007), local scale dynamics may result in increased food availability at certain locations that may not be detectable in larger scale measures of productivity. For example, terrestrial runoff discharging into a particular site may result in elevated nutrient levels and thus increased productivity. Although runoff was not prominent at most sites, Carlsbad, the site with the highest growth, is located near the Agua Hedionda Lagoon outlet that may serve as a source of nutrients and/or food. Wave activity may also play a role in determining growth at these sites and has been correlated with higher growth rates at other SCB locations (Blanchette et al., 2007). Although not directly measured, repeated observations of wave activity at sampled sites suggest that Carlsbad is the most wave-exposed followed by Treasure Island and Tuna Canyon; Carlsbad and Tuna Canyon are two of three sites with high mussel abundances and high growth. Finally, local currents may bring offshore productivity to nearshore areas leading to increased food availability as well as an increase in larval supply leading to concurrent high recruitment rates.

4.3. Conclusions

In the SCB, recruitment and growth were higher yet adult mussel abundances, even at sites with thick beds, were lower than in northern California. Differences in adult populations may be attributed to differences in mortality rates, with mussels in northern California having higher survival rates. Previous work has found regional differences in population size structures with a higher frequency of larger mussels found in northern California (Smith, 2005). In conjunction with low growth, mussels in northern California are likely much older than those in southern California. Therefore, mussel beds in northern California likely persist for a longer period of time. Southern California, on the other hand, may have higher mortality and turnover rates due to post-recruitment processes. Interestingly, the two sites with the highest recruitment and growth, Carlsbad and Tuna Canyon, qualitatively appeared to have the highest mortality rates, as indicated by observations of newly opened gaps during repeated visits (Smith pers. obs.). Furthermore, tagged mussels were more frequently lost at the sites within southern California while many tagged mussels in northern California remained for the year-long sampling period. However, it is unclear whether tagged mussels were lost due to mortality or due to loss of the tags themselves.

Recruitment and growth exhibited regional differences with both measures being important factors in driving adult populations in southern California but not in northern California. The importance of the linkage between recruitment and growth and adult populations is supported by Blanchette et al. (2006) who also found that these measures on an offshore Channel Island in the SCB were higher at sites with higher mussel cover. Contrastingly, spatial patterns of mussel abundances were not correlated with recruitment at a number of sites just north and south of Point Conception. These contrasting reports highlight the need for further studies to understand the scale of these driving factors.

Within southern California, and sometimes in close proximity (<50 km), recruitment and growth can be highly variable. Understanding local physical mechanisms underlying larval transport and growth will lead to a better understanding of adult populations and potential management of coastal species, especially those important to fisheries and local economy.

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