The impetus for this project came from the increasing attention accorded introduced seaweed species in the eastern North Pacific following the California invasions of *Caulerpa taxifolia* and *Undaria pinnatifida* around the turn of the century. Much attention was given to *Caulerpa taxifolia*, primarily because of the notoriety associated with this seaweed resulting from its problematic invasion of the Mediterranean Sea. Its appearance in two southern California inland lagoons resulted in a massive and expensive eradication effort. In contrast, the appearance of *Undaria pinnatifida*, an invader known to disrupt coastal marine communities in other parts of the world, received much less attention in California and comparable organized and well-financed efforts to totally eradicate this seaweed were not undertaken. Moreover, other introduced or likely introduced seaweeds are known from the region but their introductions have been poorly documented and little is know about their impacts on coastal communities. Some of these seaweeds appear to be very recent introductions while others have occurred in eastern North Pacific waters for many years.

This project consisted of two components with the goal of advancing our understanding of seaweed introductions in the eastern North Pacific beyond *Caulerpa taxifolia*. These included:

1) the organization and convening of a workshop focusing on the identification of research needed to improve understanding of the biology and ecology of invasive seaweeds, and

2) the funding of a small grant program to initiate small research studies on invasive seaweeds.

Both objectives were successfully achieved during the course of the project. Although funding was initially provided in 2003, the project was delayed to accommodate the timeline for developing and holding the workshop, soliciting the research proposals, and completing the one-year research studies. Workshop development was preceded by the PI, with co-authors Linda Fernandez and Jose Zertuche Gonzalez completing a report for the Center for Environmental Cooperation on threats posed in the eastern North Pacific by invasive seaweeds. This report included recommendations for management consideration that seeded discussion at the workshop. Workshop invitations were then send out and in late 2005 and the workshop convened during November of that year. During the same time period, a solicitation was made to obtain proposals to carry out the small research studies to be funded by the Pacific States Marine
Fisheries Commission grant. Proposals were to commence during January 2006 with funding to be complete by January 2007. A panel of reviewers was then convened and selections but delays in obtaining panel participants and in finalizing selection of proposals to be funded resulted in projects commencing during March 2006, a three month delay. California State University Fullerton, through its Auxiliary Services Corporation, administered the funding and set up the subcontracts for the research projects at zero indirect cost. Subcontracting administrative difficulties, however, further delayed the start dates for some of the research studies again pushing back the dates for project completion. Consequently, no-cost extensions were requested and granted and the project was not finalized until late summer 2007.

The project was overseen by Stephen Phillips for the Pacific States Marine Fisheries Commission. The PI is grateful for the opportunity to carry out this project and would particularly like to thank Stephen Phillips for his patience and understanding in accommodating several revisions to the timeframe for completing this work and serving as an advocate for the requested no-cost extensions. Project details and accomplishments are summarized below.

**Workshop**

The invasive seaweed workshop was held at the Marriott Hotel and on the CSU Fullerton campus on November 11 and 12, 2005 (Appendices 1 to 3). Assistance and support for the workshop were provided by Susan Zaleski (USC Sea Grant) and Shauna Oh (California Sea Grant). Susan Zaleski attended the workshop. The workshop was attended by 19 scientists working on introduced seaweeds (Appendix 2) plus approximately 10 CSU Fullerton faculty and students with interests in seaweed biology. Cheryl Aranda, Assistant to the Dean of the College of Natural Sciences and Mathematics (the PI), played a major role in organizing workshop logistics.

The workshop consisted of a series of presentations on the 11th followed by group and subgroup discussions on the 12th (Appendix 3). Based on informal and formal feedback from attendees, the workshop was very successful. First, almost everyone to whom an invitation was extended attended the workshop. Second, the group was unanimous in concluding that too little attention has been paid to the biology, ecology, and impacts of introduced seaweeds with only selected introduced species receiving scientific study on the west coast of North America. In addition, the group consensus that this workshop was so valuable that attempts should be made to secure funding for a future workshop on this topic.

Workshop discussions centered on the following topics:

1) What do we need to know to increase scientific understanding of introduced seaweeds with emphasis on the Pacific coast of north America? What should be the research agenda for introduced seaweeds?

2) How can we best assist managers in making decisions on how to cope with newly encountered introductions? Should we create a standing advisory group of Phycologists and a process to access this group?
Workshop attendees concluded that much remains to be learned about the biology and ecology of introduced seaweeds and made suggestions regarding research needs. Participants also discussed and reached conclusions on how to provide assistance to coastal managers charged with making decisions on how to cope with introductions. Suggested topics and questions for future research included:

1) The propagation and dispersal abilities of different seaweeds, including those with a history of establishing introduced populations. How do introduced species disperse and establish new populations?
2) The ability of seaweeds, and particular introduced seaweeds, to survive conditions in transport vectors; greater understanding of introduction pathways is needed.
3) The ecological traits of species that facilitate introduction and the genetic constraints on these traits. Can we identify candidates for possible future introductions based on ecological traits? What are the characteristics of species that do not tend to be invasive?
4) The characteristics of ecological communities that make them susceptible to invasion. Are communities predisposed for receiving invaders?
5) Identification of genetic makers for strain identification and for determining sources of introduction and frequency of introductions. Can we determine whether introductions are from single or multiple sources? Can we develop a rapid test for identifying highly invasive strains?
6) Surveys are needed to detect new introductions and determine range extensions, particularly given the current period of ocean climate change. Can we develop a cost-efficient but informative survey strategy to enable early detection of seaweed and other invaders?
7) The impacts of seaweed introductions on the structure and functioning of coastal communities need to be more fully understood. Very little work has been done on past introductions. Do introduced seaweeds out compete native seaweeds? Are introduced seaweeds less preferred or avoided by native consumers?
8) Viable eradication methods need to be developed and scientifically tested so end results can be predicted and cost and effort established. Well established populations will be difficult to eradicate but eradication might be successful on small, newly found populations or in isolated habitats. This underscores the need for early detection.

Workshop participants concluded that coastal managers could be assisted by the development of much more highly organized management structures. These structures should include a well publicized process and identified entity for receiving reports of new introductions. A panel of experts should be formed and convened, when needed, to provide advice on newly detected introductions. The panel should consist of individuals with knowledge and expertise with seaweeds, regional oceanography, and the ecology of coastal marine communities. This panel would serve as a multidisciplinary advising team to assist managers in making decisions on how to proceed once a new seaweed introduction has occurred. For example, such a panel could provide information on the potential impacts of a new introduction, its chances of spreading from locations where it has been encountered, and the likelihood that an eradication effort will be successful. This panel also would provide input into where and how science should be injected into the process. This latter panel activity acknowledges the need to take a more scientific approach when making management decisions on introductions.
Research Studies

As proposed the small seed research projects to be supported by grant funds were to include: 1) research studies to address key information needs identified during workshop discussions with specific projects to be solicited and determined through a competitive proposal process; and, 2) an initial CSU Fullerton research effort on the red seaweed *Caulacanthus ustulatus*, a new addition to southern California’s intertidal seaweed flora and a species believed to be a recent introduction. The CSU Fullerton study was established as a model in scope and size for the solicited research studies. These elements of the Pacific States Marine Fisheries Commission grant were successfully carried out and completed.

A call for proposals to serve as seed projects to stimulate research on introduced seaweeds was disseminated in late 2005 (Appendix 4). Eight proposals were received requesting more than $90,000 and distributed to four external reviewers for evaluation. Based on these reviews, the following awards were made and were administered as subcontracts to the lead PI’s institution by CSU Fullerton at zero pass through indirect cost. All projects focused on introduced seaweeds and addressed important issues of concern to the Pacific states.

Project Descriptions

Reviewers found all submitted proposals to meritorious but the proposals receiving the highest technical evaluations were funded. The PIs, study titles, and funding allocated for these projects were as follows:

*Terrie Klinger (University of Washington)* “Native consumers as agents of biotic resistance: Does the native herbivore *Lacuna vincta* reduce the invasion success of the introduced seaweed *Sargassum muticum*?” ($17,729)

*Kathy Ann Miller (University of California, Berkeley, Herbarium)* “Dispersal patterns and genetic diversity of the invasive kelp *Undaria pinnatifida* in California” ($12,152)

*Cynthia Trowbridge (Oregon State University) and Christine Maggs (Queen’s University, Belfast)* “Codium fragile ssp. tomentosoides on California shores: Current distribution and establishment ecology” ($12,347)

*Linda Walters (Central Florida University)* “Killer algae: differentiating native from invasive populations of *Caulerpa taxifolia*” ($4,784)

*Kim Whiteside and Steve Murray (California State University, Fullerton)* “Distribution, habitat utilization, and reproductive patterns in *Caulacanthus ustulatus* (Caulacanthaceae, Gigartinales), a newly established seaweed on southern California shores” ($19,168)

Summary of Results:

Summaries of the disposition of each funded proposal and the principal findings from each funded research project are listed below:
**Terrie Klinger (University of Washington) “Native consumers as agents of biotic resistance: Does the native herbivore *Lacuna vincta* reduce the invasion success of the introduced seaweed *Sargassum muticum*?”**

Dr. Klinger’s research project progressed very well and was completed in a timely manner. Dr. Klinger and her co-PI Kevin Britton-Simmons studied the response of the native, herbivorous gastropod *Lacuna vincta* on the invasive, Japanese seaweed *Sargassum muticum* in the San Juan Islands of Washington State (Appendix 5). *Lacuna vincta* reaches high abundances on *Sargassum muticum* and readily feeds on its tissues. Therefore, this snail has the potential to generate substantial biotic resistance to the *S. muticum* invasion via effects on *S. muticum* growth and reproduction. The focus of our study was how snail behavior mediated response to *Sargassum muticum* as a food and habitat resource. Specifically, we focused on three specific questions: 1) What is the aggregational (numerical) response of *Lacuna vincta* to *Sargassum muticum*? 2) Is *Lacuna vincta*’s feeding rate on *Sargassum muticum* density dependent? 3) Does *Lacuna vincta* prefer *Sargassum muticum* over native kelp species as a food resource?

Principal findings from her work included: the impact of *L. vincta* on *S. muticum* is mediated by seaweed density but not snail abundance. In addition, it is now clear that *S. muticum* is a preferred food resource in this system. Consequently, *L. vincta* may be more effective at reducing the performance of *S. muticum* in early rather than late invasion stages.

**Kathy Ann Miller (University of California, Berkeley, Herbarium) “Dispersal patterns and genetic diversity of the invasive kelp *Undaria pinnatifida* in California”**

Dr. Miller’s initial research project had to be abandoned because of the inability to set up the subcontract in time for the research to be done. This project was dependent on the availability of a key European collaborator who could not perform the anticipated analyses during the funding period. As a consequence, discussions were held with the PI and a new proposal was developed and supported and changes to the original subcontract work scope were made. This new proposal was entitled “**Studies on *Sargassum filicinum*, a new addition to the seaweed flora of southern California**”. This research focused on a newly introduced seaweed, *Sargassum filicinum* (Appendix 6). *Sargassum filicinum* Harvey (Phaeophyceae, Fucales) was first collected in October 2003 by biologists conducting surveys in inner Long Beach Harbor (33°42’N, 118°14’W). *Sargassum filicinum* was discovered through searches at Santa Catalina Island in April 2006. As a result of PSMFC funding, a return visit was made in April 2007 to study these populations in more detail. Additional reconnaissance for *S. filicinum* was performed in May 2007 with Jack Engle in a Channel Islands Research Program (CIRP) cruise to search for *S. filicinum* at Anacapa and San Clemente islands and other sites at Santa Catalina Island.

Key results of this project included: The population of *S. filicinum* near the Wrigley Marine Science Center and in its vicinity exploded during the previous year. A mean of 5 individuals per m² at depths of 5-6 m was recorded; plants formed large groves with individuals up to 2 m in length. Although juveniles were present, populations were dominated by adults bearing numerous large, fertile receptacles. *Sargassum filicinum* was absent from Anacapa Island. At San Clemente Island, a single mature 2 m long individual near the NOSC pier (32°50’N, 118°35’W), and a large patch of mature plants in a small cove just northeast of Pyramid Cove (32°48’N, 118°20’W), both on the lee side of the island were discovered. During 2006-2007, *Sargassum filicinum* spread along the lee side of Catalina, and is now common in
most coves from the east end to the west end. By mid-May, many of the mature adults were beginning to senesce though they still formed dense thickets. Carpets of juveniles were common, especially on horizontal rock surfaces at 5-6 m depth. It appears that *S. filicinum* matures quickly, recruits copiously, has a short life span but produces overlapping generations.

**Cynthia Trowbridge (Oregon State University) and Christine Maggs (Queen’s University, Belfast) “Codium fragile ssp. tomentosoides on California shores: Current distribution and establishment ecology”**

Dr. Trowbridge’s research unfortunately had to be abandoned because of changes in her status at Oregon State University; after submitting her proposal, Dr. Trowbridge was no longer able to secure the needed space and university support to carry out her work. Allocated funds had to be retrieved and were reassigned to support two projects: additional studies of introduced seaweeds at CSU Fullerton and central Florida and outreach activities to increase public awareness of introduced species of *Caulerpa* being performed at the University of Southern California by Susan Zaleski. Of the funding allocated to Dr. Trowbridge’s project, $4,800 was allocated to support outreach on introduced seaweeds carried out by USC Sea Grant under the direction of Susan Zaleski. Outreach efforts were designated as very important by workshop participants. Funds were used for the duplication of outreach DVDs (see website with all the outreach info and animation: [http://www.usc.edu/org/seagrant/caulerpa/index.html](http://www.usc.edu/org/seagrant/caulerpa/index.html)). The remaining funds were used to purchase supplies and expendable equipment to support either the CSU Fullerton project on *Caulacanthus ustulatus* or Dr. Walter’s research project on fragmentation and fragment viability in *Caulerpa* and other aquarium species.

**Linda Walters (Central Florida University) “Killer Algae: Differentiating Native from Invasive Populations of *Caulerpa taxifolia*”**

Dr. Walter’s research project needed to be re-focused after it was learned that some of the planned experiments were already being run by others. The project was modified to address minimum fragment size and fragment retention in the field with *Caulerpa taxifolia*. This research was successfully completed. The goal for this project was to focus on one question posed by the *Caulerpa* Working Group that helped develop the National *Caulerpa* Management Plan. The question they posed and which was addressed was very straight-forward, “What is the smallest viable size fragment of native versus invasive *C. taxifolia*?”. All experiments were run in Australia where both native and invasive populations occur. This information is critical to resource managers around the globe responsible for monitoring both invaded and un-invaded sites, as well as for individuals involved in eradication efforts. It is also very important for outreach specialists working with the aquarium industry to prevent future introductions.

Principal findings included (Appendix 7): Both the native and invasive strains of *C. taxifolia* had frond tip fragments as small as 4 mm that were able to survive cutting damage and produced new attachment structures in laboratory bioassays. Stolon fragments had to be 15 – 20 mm in length to survive. Blade and stolon fragments greater than 20 mm in length were regularly produced in both locations, most likely by human activities and winds. Many fragments are then retained in *Zostera* and *Caulerpa* beds in Lake Conjola and Moreton Bay. In one case, a fragment was retained in a bare patch of substrate after being partially buried by a polychaete worm.
Kim Whiteside and Steve Murray (California State University, Fullerton)  
“Distribution, Habitat Utilization, and Reproductive Patterns in Caulacanthus ustulatus (Caulacanthaceae, Gigartinales), a Newly Established Seaweed on Southern California Shores”

Kim Whiteside and Dr. Murray’s project was carried out smoothly and progressed well (Appendix 8). **Caulacanthus ustulatus**, a cryptogenic red algal turf-forming species, was first reported in southern California in 1999. This species had previously been reported in the Northeastern Pacific only from Baja California, Washington, British Columbia, and three isolated localities in California. Molecular studies indicate that specimens from Washington and southern California are identical to material from Asia, and from northern France where the species has been introduced. Its absence from previous surveys and its genetic affinity with Asian specimens suggests that southern California populations of **Caulacanthus** may not be indigenous. The project focused on southern California populations of **Caulacanthus** with the goals of determining its: 1) current southern California distribution, 2) abundance and habitat utilization at local sites, and 3) reproductive patterns.

Principal results of this project included: Our surveys and specimens obtained from colleagues revealed that **Caulacanthus** is widespread along the southern California mainland from Los Angeles County to San Diego Bay and on both Catalina and Anacapa Islands. Abundance sampling at two Orange County locations over the last four years has shown that **Caulacanthus** is confined to mid and upper intertidal habitats where it is a persistent contributor to cover in algal turf communities. **Caulacanthus** grows on a variety of substrata including rock, mussel and barnacle surfaces, turf-forming macro-algae, and rockweed bases. Examination of thalli from local sites revealed that the majority of **Caulacanthus** specimens are sterile but that tetrasporangial plants exist, suggesting that both vegetative and spore recruitment are likely mechanisms for dispersal.

**Presentations and Publications Resulting from the Project**

A total of 11 presentations, 2 published abstracts, 1 technical report, and 2 student theses were supported by funding provided by the project. Several public lectures and seminars also were given by the PI and by Linda Walters based on results of PSMFC funding. Additional presentations and publications, including peer-reviewed journal publications, resulting from the research supported by this project are certain; all such publications will acknowledge the Pacific States Marine Fisheries Commission and California State University Fullerton as funding sources.

**Presentations**


Whiteside, K. E., A. M. Bullard, and S. N. Murray. California State University, Fullerton. Distribution, abundance, habitat utilization, and reproductive patterns in *Caulacanthus ustulatus* (Caulacanthaceae, Gigartinales) a newly established seaweed on southern California shores.” Western Society of Naturalists 86th Annual Meeting Seaside, CA November 2005.

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

Abstracts


Technical Reports

Student Theses

Whiteside, K. E. (In Preparation). Distribution, abundance, habitat utilization, and reproductive patterns in Caulacanthus ustulatus (Caulacanthaceae, Gigartinales) a newly established seaweed on southern California shores M.S. Thesis, California State University, Fullerton.
Appendix 1.

WORKSHOP
ESTABLISHING A RESEARCH AGENDA FOR INTRODUCED SEAWEEDS

California State University Fullerton
November 11 and 12, 2005
Workshop Organizer: Steve Murray

Invitation

I would like to invite you to participate in a workshop on introduced seaweeds to be held at California State University Fullerton on November 11 and 12, 2005. This workshop, which is supported by the Pacific States Marine Fisheries Commission (PSMFC) with assistance from the California Sea Grant and the University of Southern California Sea Grant Programs, will focus on identifying research needed to improve understanding of the biology and ecology of introduced seaweeds, with emphasis on species introduced to California waters. Funds are available to cover your transportation costs, lodging, and meals.

This workshop will bring together a small group of mostly west-coast scientists with knowledge and expertise for two days of presentations and discussions. In addition to identifying research needs, strategies for more effectively assisting coastal managers in dealing with newly detected seaweed introductions will be discussed. A workshop schedule is being developed.

To allow for workshop planning, please let us know if you will be able to participate by contacting Steve Murray (email smurray@fullerton.edu; phone 714-278-2638) by October 1.

Rationale

The appearance of Caulerpa taxifolia, a few years ago at two southern California sites was well publicized and led to a costly eradication effort. As you know, this highly invasive seaweed gained notoriety due to its rapid spread and its effects on native benthic communities in the Mediterranean Sea. Other non-native seaweeds also have recently been detected in Californian waters. For example, the kelp, Undaria pinnatifida now occurs in southern and central California ports, at a site 20 to 30 m depth off Santa Catalina Island, and in Mexican waters near Ensenada. Although less well publicized, U. pinnatifida, like Caulerpa taxifolia, has the potential to alter ecosystem structure and functioning, perhaps by outcompeting native species of kelps and other seaweeds. During this same period, another seaweed, Caulacanthus ustulatus, began to grow abundantly in mid-shore habitats on southern California shores where it had never before been detected. Molecular analyses indicate that California specimens belong to the same genetic strain that recently invaded Brittany, suggesting that C. ustulatus also has been introduced into Californian waters. Other seaweeds, such as Sargassum muticum and Lomentaria hakodatensis, are well known introductions, but have received remarkably little scientific
attention in California despite being quite abundant along certain portions of the coast. Many other seaweeds are cryptogenic, i.e., species that are neither demonstrably native nor introduced. This workshop is timely given the potential for introduced seaweeds to impact coastal ecosystems and the documented increase in marine introductions taking place in California and throughout the United States.

Workshop Details

The workshop will be conducted on the California State University campus and begin at 9:00 AM November 11 (Friday) and conclude at 3:00 PM November 12 (Saturday). The Fullerton campus is located in the city of Fullerton in northern Orange County near the cities of Anaheim, Yorba Linda, Placentia, and Brea. Three airports are convenient to the campus: Los Angeles International Airport, Orange County (Santa Ana) John Wayne Airport, and Ontario Airport. Airport shuttle services run directly to the Marriott Fullerton, a hotel located on the southeast corner of the campus at 2701 East Nutwood Avenue, Fullerton, California 92831.

It is anticipated that most participants will arrive Thursday and be able to depart Saturday evening. A group dinner is scheduled for Friday evening.

Lodging. A block of rooms has been reserved at the discounted rate of $99 (plus appropriate taxes) per night at the Marriott Hotel under the event name of Seaweed Workshop. You will need to reserve your room by contacting the Marriott directly at 1-800-228-9290 or 714-738-7800 and hold your reservation with a credit card. PLEASE NOTE THAT ALL HOTEL RESERVATIONS MUST BE MADE BY OCTOBER 20.
Appendix 2.

WORKSHOP
ESTABLISHING A RESEARCH AGENDA FOR INTRODUCED SEAWEEDS

California State University Fullerton
November 11 and 12, 2005

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Appendix 3.

WORKSHOP
ESTABLISHING A RESEARCH AGENDA FOR INTRODUCED SEAWEEDS

California State University Fullerton
November 11 and 12, 2005

Sponsored by the Pacific States Marine Fisheries Commission and California State University, Fullerton with assistance and support from the University of Southern California Sea Grant and California Sea Grant Programs

November 11 (Friday)

Morning Session: Marriott Hotel (Salon A)

900   Introductions and Welcome to the Workshop – Steve Murray and Others

930   Seaweed Introductions: An Overview - Steve Murray, California State University, Fullerton

1000  A Survey for Introduced Seaweeds in California – Erin Maloney, Moss Landing Marine Laboratories

1030  Update on the Caulerpa taxifolia Eradication Program in Southern California – Rachel Woodfield, Merkel and Associates

1100  Monitoring and management of the Asian kelp Undaria pinnatifida in Monterey Harbor – Steve Lonhart, Monterey Bay National Marine Sanctuary

1130  A View on Introduced Seaweeds and Introductions from the California Department of Fish and Game – Susan Ellis, California Department of Fish and Game

1200  Lunch

Afternoon Session: Cal State Fullerton (MH 121)

130   Caulerpa: history, availability, education and outreach – Linda Walters, University of Central Florida

200   An overview of Undaria pinnatifida invasion and impacts – Mike Graham, Moss Landing Marine Laboratories
The invasive seaweed *Sargassum muticum*: known knowns, known unknowns and unknown unknowns – Kevin Britton-Simmons, Friday Harbor Laboratories, University of Washington

Break

Codium fragile ssp. tomentosoides: review and prospectus – Cynthia Trowbridge, Oregon State University

Distribution, habitat utilization, productivity, and reproductive patterns in *Caulacanthus ustulatus*, a newly established seaweed on southern California shores – Kim Whiteside, Aimee Bullard, and Steve Murray, California State University, Fullerton

Group Discussion – Introduced Seaweeds: Wrap up. What do we know? What do we need to know?

Dinner at Steve Murray’s House

**November 12 (Saturday): Cal State Fullerton (MH 121)**

8:30 Group Discussion – What do we need to know to increase scientific understanding of introduced seaweeds with emphasis on the Pacific Coast of North America?

9:15 Subgroup Discussions: Establishing research agendas for introduced seaweeds (Locations to be announced)

*Undaria* Subgroup

*Caulerpa* Subgroup

*Sargassum/Codium/Caulacanthus* subgroup

11:15 Subgroup Reports (MH 121)

12:00 Lunch

1:00 Group Discussion (MH 121) – How can we best assist managers in making decisions on how to cope with newly encountered introductions? Should we create a standing advisory group of Phycologists and a process to access this process?

2:30 Workshop Wrap up

3:00 Departure
Appendix 4.

GRANT OPPORTUNITY
RESEARCH ON INTRODUCED SEAWEEDS

The appearance of Caulerpa taxifolia, a few years ago at two southern California sites was well publicized and led to a costly eradication effort. This highly invasive seaweed gained notoriety due to its rapid spread and its effects on native benthic communities in the Mediterranean Sea. Other non-native seaweeds also have recently been detected in Californian waters. For example, the kelp, Undaria pinnatifida now occurs in southern and central California ports, at a site 20 to 30 m depth off Santa Catalina Island, and in Mexican waters near Ensenada. Although less well publicized, U. pinnatifida, like Caulerpa taxifolia, has the potential to alter ecosystem structure and functioning, perhaps by out competing native species of kelps and other seaweeds. During this same period, another seaweed, Caulacanthus ustulatus, began to grow abundantly in mid-shore habitats on southern California shores where it had never before been detected. Molecular analyses indicate that California specimens belong to the same genetic strain that recently invaded Brittany, suggesting that C. ustulatus also has been introduced into Californian waters. Other seaweeds, such as Sargassum muticum and Lomentaria hakodatensis, are well known introductions, but have received remarkably little scientific attention in California despite being quite abundant along certain portions of the coast. Many additional seaweeds are cryptogenic, i.e., species that are neither demonstrably native nor introduced.

Improved understanding of the biology of non-native seaweeds is crucial, given the potential for introduced seaweeds to impact coastal ecosystems and the documented increase in marine introductions taking place in California and throughout the United States. To address this research need, a total of $45,000 has been provided by the Pacific States Marine Fisheries Commission (PSMFC) to be disseminated by California State University Fullerton to support research projects on introduced seaweeds.

Proposal Restrictions

Proposals are solicited to carry out research on any problem dealing with introduced seaweeds. Individual proposals should cost no more than $20,000 and are restricted to research elements that can be completed within one year. Funds can be used for salaries and fringe costs, expendable equipment and supplies, and travel; expenditures for permanent equipment are not allowed. IDC costs on grants are limited to the official off-campus rate. Matching funds are encouraged but not required.
Proposal Format

Proposals are limited to 5 single space pages (12 point font), excluding Literature Cited and Budget pages, and include the following sections: 1) Introduction providing the rationale for the project; 2) Purpose and Hypotheses or Research Questions; 3) Study Design and Methods; 4) Significance of the Research; 5) Literature Cited; 6) Budget and Budget Justification. Margins should be approximately one inch and type lines should be left justified.

Instructions for Submission

An electronic (minus signatures) and two hard copies of a complete proposal are required. The original proposal should be sent to your campus research office for approval and then forwarded along with one additional copy to:

RESEARCH ON INTRODUCED SEAWEEDS
Dr. Steve Murray
Dean, College of Natural Sciences and Mathematics
California State University Fullerton
Fullerton, CA 92834-6850
FAX: 714-278-5390

Proposals are due by 5:00 PM November 1, 2005 with funding to commence by January 1, 2006. All funds are to be expended by December 31, 2006. A final project report is due on January 15, 2007.

For additional information on this grant opportunity, please contact Steve Murray by phone (714-278-2638) or email: (smurray@fullerton.edu).
Appendix 5.

Native consumers as agents of biotic resistance
Kevin Britton-Simmons and Terrie Klinger
University of Washington

INTRODUCTION

The capacity of native communities to resist invasion by non-indigenous species has been the subject of considerable work during the past decade. The vast majority of biotic resistance studies have focused on the importance of competitors in generating invasion resistance (see reviews by Levine et al. 2004 and Levine and D’Antonio 1999). Studies of predation, on the other hand, have been structured in the context of the enemy release hypothesis (ERH), which posits that non-native species should experience less regulation by predators, parasites and pathogens in their introduced range (Darwin 1859, Elton 1958, Williamson 1996, Keane and Crawley 2002). In theory this “enemy release” should allow invaders to reduce investments in defenses and redirect that energy to growth and reproduction, which should give them an advantage over the native species with whom they compete for resources.

Although many studies appear to support the predictions of the ERH (e.g. Dewalt et al. 2004, Mitchell and Power 2003, Carpenter and Cappuccino 2005, Vila et al. 2005), recent reviews have not only called into question its broad explanatory power (Colautti et al. 2004, Levine et al. 2004) but have suggested that native predators may actually be an important source of biotic resistance to invading species in some systems (Levine et al. 2004, Parker and Hay 2005). A large number of studies have documented the consumption of introduced species by native consumers and it increasingly appears that this is a common phenomenon (Prince and LeBlanc 1992, Rilov et al. 2002, Trowbridge 2004, Parker and Hay 2005, and many others). However, the effect of native consumers on the success of their invasive prey is poorly understood, particularly in marine ecosystems.

We studied the response of the native, herbivorous gastropod Lacuna vincta on the invasive, Japanese seaweed Sargassum muticum in the San Juan Islands of Washington State. Lacuna vincta reaches high abundances on Sargassum muticum and readily feeds on its tissues (Britton-Simmons, unpublished). Therefore, this snail has the potential to generate substantial biotic resistance to the S. muticum invasion via effects on S. muticum growth and reproduction. The focus of our study was how snail behavior mediated response to Sargassum muticum as a food and habitat resource. Specifically, we focused on three specific questions: 1) What is the aggregational (numerical) response of Lacuna vincta to Sargassum muticum? 2) Is Lacuna vincta’s feeding rate on Sargassum muticum density dependent? 3) Does Lacuna vincta prefer Sargassum muticum over native kelp species as a food resource?
METHODS

*Aggregational Response of *L. vincta*

We measured the aggregational (numerical) response of *L. vincta* to *S. muticum* by quantifying the abundance of *L. vincta* on *S. muticum* across a range of *S. muticum* patches that varied in density. At each of 4 study sites within the San Juan Islands (see Fig. 1 for place names) we collected *S. muticum* plants underwater by enclosing them in plastic bags that were then sealed with cable ties. Plants were sampled from *S. muticum* patches that spanned the range of patch densities present at each site by collecting samples from predetermined density intervals that were used for sampling at all sites. Between 26 and 31 plants were collected at each site for a total of 115 samples. Some of the predetermined *S. muticum* density intervals did not occur at all sites. Bagged plants were returned to the laboratory where we counted the number of *Lacuna vincta* on each plant and measured the wet mass and length of each *S. muticum*.

*Density Feeding Trial*

We used a laboratory feeding experiment in which we manipulated snail density in order to determine whether the per capita feeding rate of *Lacuna vincta* on *Sargassum muticum* is density dependent. We measured the per capita feeding rate of *L. vincta* across a range of snail densities that bracket the densities found in the field (treatment levels: 2, 5, and 10 snails per g of *S. muticum* tissue). The wet mass of *S. muticum* tissue was determined at the beginning and end of the experiment and a control treatment without snails was used to account for seaweed growth in the absence of snails. Each treatment was replicated 11 times.

*Preference Feeding Trial*

We performed a feeding preference experiment using artificial foods to validate the results of a previous feeding trial that was carried out using fresh tissue. Tissues of *S. muticum*, in addition to two native kelp species *Saccharina subsimplex* and *Agarum fimbriatum* were freeze-dried and ground to a powder. We then used this material to make artificial agar foods containing the ground tissue from each species in order to assess *L. vincta* feeding preferences without the potentially confounding influence of among-species differences in algal morphology. A control (agar only) treatment was used to determine changes in mass not due to feeding. Each treatment was replicated 12 times. We measured feeding on the artificial foods by weighing the artificial food blocks before and after the *L. vincta* were allowed to feed on them.
RESULTS

Figure 1. Relationship between snail abundance and *S. muticum* patch density at four sites (n=115).

*Aggregational Response of L. vincta*

Sampling was performed at 4 field sites and although the sites differed somewhat in the range of *S. muticum* densities they contained, the relationship between *S. muticum* patch density and snail density was consistent across all sites. At low patch density snail abundance was highly variable, with some patches having high snail densities and some having low snail densities. In contrast, at high patch density abundance of *L. vincta* was low (Fig. 1).

*Density Feeding Trial*

There was no difference in per capita feeding rate among the snail density treatments (one-way ANOVA, P = 0.81, Fig. 2). These results indicate that *Lacuna vincta* feeding rate is density independent (i.e., feeding rate is not reduced at high snail density).
Figure 2. Per capita consumption of *S. muticum* by *Lacuna vincta* across the range of snail densities found in the field.

**Feeding Preference Trial**

Snails showed a preference for some artificial foods over others (Kruskal-Wallis, H2 = 12.85, P < 10^{-4}, Fig. 3). Post-hoc comparisons of the means indicated that artificial foods made from *S. muticum* were preferred significantly over those made from both *A. fimbriatum* and *L. bongardiana* (Fig. 3). However, artificial foods made from the two native kelp species were equally preferred (Fig. 3).

Figure 3. Consumption by *Lacuna vincta* of artificial foods made from *S. muticum* and two native kelp species in a feeding preference trial.
DISCUSSION

The numerical response data indicate that *L. vincta* is capable of reaching extremely high densities when *S. muticum* is at very low patch density. However, in high density *S. muticum* patches *Lacuna* was never abundant (Fig. 1). We suggest two non-exclusive mechanisms that could generate this pattern. First, a dilution effect may occur in high density *S. muticum* patches because high density patches also tend to be larger, have a smaller perimeter to area ratio and therefore may “trap” fewer snails than do smaller, low density patches (Kunin 1999). Second, predators of *Lacuna vincta*, which include kelp crabs (*Pugettia spp.*) and fishes (Embiotocidae), may preferentially forage in high density patches of *S. muticum* and thereby reduce snail density in those patches. Regardless of the underlying mechanism, this pattern suggests that incipient *S. muticum* invasions are unlikely to escape herbivory by *L. vincta*. Conversely, dense *S. muticum* patches are like to escape intense herbivory because *L. vincta* is less abundant in those patches.

When consumers reach high densities their per capita feeding rate can be reduced due to a variety of density dependent interactions, including agonistic encounters and reproduction. Interestingly, the per capita feeding rate of *L. vincta* was not influenced by snail density across the range of snail densities found in the field (Fig. 2). This result suggests that the damage caused by *L. vincta* herbivory when it is at high abundance in the field will not be modulated by snail density.

In a previous feeding preference experiment we found that *L. vincta* preferred to consume *S. muticum* over the two most common native kelps (*L. bongardiana* and *A. fimbriatum*). However, this feeding trial used fresh, intact algal tissue and our results were therefore potentially confounded by morphological differences among the algal species. For example, *S. muticum* has a very wiry morphology with a high surface area to volume ratio compared to either of the native kelps, which could have made its tissues more accessible to grazing. We eliminated the effects of these morphological differences by performing a feeding trial in which we used artificial foods made from the three species of algae. The results from this new feeding trial support those from the experiment carried out with fresh tissue: *L. vincta* prefers *S. muticum* over both native kelp species. In summary, our research suggests that the impact of *L. vincta* on *S. muticum* is mediated by seaweed density but not snail abundance. In addition, it is now clear that *S. muticum* is a preferred food resource in this system. Consequently, *L. vincta* may be more effective at reducing the performance of *S. muticum* in early rather than late invasion stages.

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Appendix 6.

*Sargassum filicinum* Harvey (Phaeophyceae, Fucales): a new invasive seaweed in the California Channel Islands

Kathy Ann Miller
University of California Berkeley

**INTRODUCTION**

*Sargassum filicinum* Harvey (Phaeophyceae, Fucales) was first collected in October 2003 by biologists conducting surveys in inner Long Beach Harbor (33°42’N, 118°14’W) (Marine Biological Consultants, pers. comm.). By October 2005, the population had spread within Long Beach Harbor, occurring on both the Terminal Island and the Long Beach side of the channel (Marine Biological Consultants, pers. comm.). The Long Beach plants were attached to the substrate or epiphytic on *Sargassum muticum*. I examined small specimens, lacking vesicles, and identified them as *Sargassum horneri* (Turner) C. Agardh, an Asian species very closely related to *S. filicinum* (Yoshida 1983; Stiger et al. 2003).

Both *Sargassum horneri* and *S. filicinum* have deeply incised, often notched vegetative leaves with spiny branches, but mature *S. horneri* bears cylindrical vesicles while those of *S. filicinum* are spherical to elliptical (Yoshida 1983; Tseng et al. 1985; Fig. 3a and 3b). *Sargassum horneri* is broadly distributed in Japan, Korea, Hong Kong, Taiwan and China (Tseng et al. 1985), often forming extensive meadows in sheltered areas, while *S. filicinum* has a narrower distribution in western Japan (Yoshida 1983; Tseng et al. 1985) and Korea (Lee & Yoo 1992).

*Sargassum filicinum*, like its congener *S. muticum*, a successful world-wide invasive seaweed, is well adapted for widespread dispersal to and rapid colonization of new areas (Nyberg & Wallentinius 2005). Fertile fragments are buoyant due to air-filled vesicles and can readily disperse locally. Like *S. muticum*, this species is monoecious, bearing both male and female conceptacles; individuals are thus capable of self-fertilization. Its establishment, like that of *S. muticum* and *Undaria pinnatifida*, may be promoted by its precocious fertility, which is presumably related to its essentially annual growth pattern.

I discovered *Sargassum filicinum* at Santa Catalina Island in April 2006. I returned in April 2007 to study these populations in more detail. In May 2007, I joined Jack Engle in a Channel Islands Research Program (CIRP) cruise to search for *S. filicinum* at Anacapa and San Clemente islands and other sites at Catalina. The presence of *S. filicinum* at the islands is important, since they are not exposed to international shipping as vectors, and since the habitats there are pristine relative to those on the mainland.
MATERIALS AND METHODS

April 2006

I collaborated with Hiroshi Kawai and Shinya Uwai (Kobe University, Japan), who compared Catalina samples of \textit{S. filicinum} to Japanese samples using the \textit{cox3} molecular marker. This report, confirming the identity of this species, was submitted to \textit{Biological Invasions} (Miller et al. 2006).

April 2007

My students in the Marine Conservation Biology class (Three Seas Marine Biology Program) and I surveyed the Isthmus area (west end, lee side) of Catalina Island. We measured density, age class, length and biomass of \textit{S. filicinum} at three sites in the vicinity of the Wrigley Marine Science Center.

May 2007

Six divers surveyed 15 subtidal sites at Anacapa, San Clemente and Catalina islands with SCUBA, spending 40-60 minutes at each site.

RESULTS AND DISCUSSION

April 2006

On 8 April 2006, I discovered a population of \textit{Sargassum filicinum} at the Intake Pipes (33°26’N, 118°29’W), a rocky point north of Big Fisherman Cove near the University of Southern California’s Wrigley Marine Science Center (WMSC) and the town of Two Harbors, on Santa Catalina Island, CA. There were more than 30 plants (0.3-1.5 m tall) at depths between 4-12 m, some of which were young, with symmetrical, spiny leaves and many of which were mature, bearing elongate receptacles and the characteristic spherical-elliptical vesicles of \textit{Sargassum filicinum}. Individuals were also observed in sheltered habitats at Cherry Cove (2 plants at 4 m and 13 m depths) and Emerald Bay (4 plants at 7 m depth), both nearby sites on the leeward west end of the island (1.8 km and 3.0 km NW of Intake Pipes).

April 2007

The population of \textit{S. ficinum} near the WMSC and in its vicinity exploded during the previous year. We measured a mean of 5 individuals per m$^2$ at depths of 5-6 m, forming large groves with plants up to 2 m in length. Although juveniles were present, populations were dominated by adults bearing numerous large, fertile receptacles. Details of this study will be presented in another paper.
May 2007

*Sargassum filicinum* was absent from Anacapa Island. At San Clemente Island, we found a single mature 2 m long individual near the NOSC pier (32°50’N, 118°35’W), and a large patch of mature plants in a small cove just northeast of Pyramid Cove (32°48’N, 118°20’W), both on the lee side of the island. This is the first report of the occurrence of *S. filicinum* at San Clemente Island.

During 2006-2007, *Sargassum filicinum* has spread along the lee side of Catalina, and is now common in most coves from the east end to the west end. By mid-May, many of the mature adults were beginning to senesce though they still formed dense thickets. Carpets of juveniles were common, especially on horizontal rock surfaces at 5-6 m depth. It appears that *S. filicinum* matures quickly, recruits copiously, has a short life span but produces overlapping generations.

_In Progress_

I will present these finding at the California islands Symposium in February 2008. I will also summarize these results, with additional details, in an update paper for *Biological Invasions*.

**ACKNOWLEDGMENTS**

I am extremely grateful to the California State University at Fullerton and the Pacific States Marine Fisheries Commission for funding my travel to Santa Catalina Island, my participation in the cruise to the islands and my workup of these results. This work would not be possible without their support. Thanks also to Jack Engle and the Tatman Foundation for diving and boat support.

**LITERATURE CITED**


MBC Applied Environmental Sciences, 3000 Redhill Avenue, Costa Mesa, CA 92626

Miller, KA, Engle, JA, Uwai, S, Kawai, H. 2006. First Report of the Asian Seaweed *Sargassum filicinum* Harvey (Fucales) in California, USA. *Biological Invasions*. Published online: 11 November 2006


Appendix 7.

Minimum Fragment Size of Native Versus Invasive Strains of the Marine Macroalga Caulerpa taxifolia

Linda Walters
University of Central Florida

INTRODUCTION

Caulerpa taxifolia (Vahl) C. Agardh (Caulerpales, Chlorphyta) is a marine macroalga with multiple upright, feathery blades, and a basal rhizome (stolon) that runs across the sandy or muddy bottom which is anchored to the substrate by bundles of colorless, filamentous, root-like rhizoids. Growth is indeterminate in this species (Collado-Vides and Robledo 1999) and it is native to subtidal waters in tropical and sub-tropical areas in the Caribbean, Indonesia, Southeast Asia, Australia and Hawaii (Phillips and Price 2002). In these waters, it can be found as isolated individuals on reef flats (e.g. Hawaii), attached to the undersides of docks (e.g. Coconut Island, Hawaii) or in a distinct, narrow band in soft sediments immediately seaward the low tide line (e.g. Moreton Bay, Australia) (pers. obs.). More commonly, C. taxifolia is known by the aquarium industry as “feather Caulerpa” or “feather algae”. As such, it is lumped with a number of other species of Caulerpa with feathery blades (C. sertularioides, C. ashmeadii, C. mexicana) and this group has dominated the flora in both personal and public salt water aquaria for decades (Walters et al. 2006).

The invasion history of the aquarium strain of Caulerpa taxifolia (a.k.a. the killer alga) started with its accidental introduction into the Mediterranean Sea while cleaning tanks at the Monaco Oceanographic Museum in 1984 (Meinesz and Hesse 1991, Meinesz et al. 2001). Initial reports documented expansion from a small patch adjacent to the Museum to many additional areas, initially increasing at a rate of 50 kilometers per year (Meinesz et al. 1993). Monocultures of the aquarium strain of C. taxifolia can now be found at over 100 locations extending for hundreds of kilometers along the Mediterranean coastline extending from French Catalonia (1991), the Balearic Islands (1992), Sicily (1993), Tunisia (1994), Croatia (1994) and the spread continues to this day (Meinesz et al. 2001). Through DNA forensics, the global origin of this invasive strain was found to be Moreton Bay in Queensland, Australia (Wiedenmann et al. 2001). In particular, it was imported in the early 1970s by the Wilhelmina Zoologischbotanischer Garden in Stuttgart, Germany which displayed the plant in its tropical aquarium (Jousson et al. 1998). Between 1980 and 1983, this strain was given to the tropical aquarium of Nancy (northern France) and subsequently to Monaco’s Oceanographic Museum on the Mediterranean coast (Jousson et al. 1998). Thus, it was cultivated in aquaria for 10-14 years prior to being found in Monaco waters (Jousson et al. 1998).

In 1992/1993, invasive C. taxifolia was found in the Sea of Japan, probably as a result of an aquarium release (Komatsu et al. 2003). However, the mean surface water
temperature in the winter of 1993 dropped to 9.8°C for two months and, for this or some other unknown reason, *C. taxifolia* did not become established (Komatsu et al. 2003). Populations of *C. taxifolia* were discovered in April 2000 in Port Hacking near Sydney, Australia (Schaffelke et al. 2002), more than 800 kilometers south of their native distribution. Also in April 2000, it was found 200 km south of Sydney in Lake Conjola. It is likely that these invasions occurred up to 2 years prior (Port Hacking) or between 5 and 13 years earlier (Lake Conjola) (Creese et al. 2004). In Australia, the number of invaded locations continues to increase with nine coastal lakes/estuaries in New South Wales and two additional waterways in South Australia now extensively invaded (Schaffelke et al. 2002; Millar 2004). In NSW, Lake Conjola is the most severely infested location (West and West 2007). Average densities of *C. taxifolia* at invaded sites in Australia are the highest recorded globally, with 4700 stolons and 9000 fronds per square meter (Wright 2005). Using molecular markers, Schaffelke et al. (2002) and Murray and Schaffelke (2003) ruled out that *C. taxifolia* was introduced from overseas (Mediterranean or other overseas aquaria) with high confidence for 3 of the 6 new locations. Most likely the new locations are the result of domestic translocation(s) from Australian subtropical populations assisted by human activities, as boating, fishing and the domestic aquarium trade (Schaffelke et al. 2002, Schaffelke et al. 2006). In 2000, populations of the aquarium strain of *C. taxifolia* were also found in two lagoons in southern California (Jousson et al. 2000; Anderson 2005). To date, *Caulerpa taxifolia* has only been completely eradicated in United States waters. A large celebration was held on 12 July 2006 to savor this victory in spite of the price tag of over seven million dollars and the necessary ecological travesty associated with adding high doses of chlorine to the infested estuaries (Anderson 2005; R. Woodfield, pers. com.).

One hallmark of an invasive species is its ability to rapidly spread both to close and distant locations. Short range expansion in *Caulerpa* occurs regularly via the basal rhizome. Like many genera of marine macroalgae, members of the genus *Caulerpa* excel at longer range expansion via vegetative fragmentation (Smith and Walters 1999, Vroom and Smith 2001, Herren et al. 2006). For this type of asexual reproduction to be important, fragments must be regularly generated, and these fragments must have the ability to disperse widely, land safely and then rapidly attach and grow under a new suite of biotic and abiotic conditions (Smith and Walters 1999). Smith and Walters (1999) found that *C. taxifolia* from Hawaii grew from fragments as small as 1 cm of frond. With the genus *Caulerpa*, this capability is especially impressive as all members of the genus are siphonous, meaning that there are no internal cell walls to reduce loss of cytoplasm when damage occurs to an individual. Long before this genus became well known as an invasive species, research on *Caulerpa* (*C. simpliciuscula, C. ashmeadii*) was focused on understanding the underlying chemical properties that healed wounds in less than 1 min and kept fragments or the parent thallus from losing all nucleus-rich cytoplasm needed for survival (Dreher et al. 1978; Goddard and Dawes 1983).

My goal for this project was to focus on one question posed by the *Caulerpa* Working Group that helped develop the National *Caulerpa* Management Plan. The question they posed and I addressed was very straight-forward, “What is the smallest viable size fragment of native versus invasive *C. taxifolia*?” All experiments were run in
Australia where both native and invasive populations occur. This information is critical to resource managers around the globe responsible for monitoring both invaded and un-invaded sites, as well as for individuals involved in eradication efforts. It is also very important for outreach specialists working with the aquarium industry to prevent future introductions.

**METHODS**

*Fragmentation Bioassays*

Laboratory trials were conducted with *C. taxifolia* collected from Lake Conjola, New South Wales, Australia and from One Mile Harbor, Moreton Bay, Queensland, Australia. The former represents an invaded site while the latter is a native population, and thought to be the likely source of the invasive, Mediterranean aquarium strain (Wiedenmann et al. 2001). Methods used at both sites were similar. In each of three trials at each site, there were 12 replicates of stolon tip and frond tip fragment sizes and all were created with a single edge razor blade (lengths: 2, 4, 6, 8, 10, 15, 20 mm). All were placed in separate wells of polystyrene, 12-well plates with 5 ml of locally collected seawater (salinity 34-35 ppt) placed on top of white sheets that were next to large windows in 22-25°C rooms. Water temperature was similar at the collection locations during our study (Table 1). Water in dishes was carefully replaced every other day during each trial. Fragment survival and new growth were recorded daily for 8 days. Fragments were considered alive if they remained turgid when probed with forceps and retained at least some green coloration (Smith and Walters 1999).

*Fragment Abundance in Field*

To compliment our understanding of fragment success, information was needed on the abundance and size of these negatively buoyant fragments in both waterways. Immediately upon arrival on each visit at both sites, all fragments of *C. taxifolia* in a 30 X 2 m band transect along the tide line were collected. All fragments were traced on transparency sheets and then disposed of onshore so as to not re-enter the fragment pool. Maximum wind speed, salinity, number of boats per hour and temperature were also recorded each day. Maximum wind speed was recorded with a Kestrel 2000 wind gauge and was averaged over a 3-min period each day.

*Fragment Retention*

Two trials were designed to monitor retention of fragments in local habitat types. The first involved deploying live fragments of specific sizes we created in each habitat type. Although this worked well in preliminary trials in the Florida Keys with *Caulerpa sertularioides*, it was not successful in Lake Conjola due to the huge fragment pool at this location. Instead, trials with mimics created from colored flagging tape (6 mm wide X 20 or 40 mm length) were run. In each of six 0.25 m² quadrats of 1) sand, 2) the seagrass *Zostera capricorni* (short shoot number ranged from 19-40), 3) low density (20 – 30 g wet weight biomass) and 4) high density (82-200 g) patches of *Caulerpa taxifolia*, we deployed 5 mimic fragments of each size that were individually numbered. All quadrats were at 1 m depth and separated by a minimum of 2 m. Mimic retention in each quadrat
was recorded after 4 days. The distance mimics were dispersed outside of their initial quadrats was also recorded after 4 days. Three trials were run in Lake Conjola and in Moreton Bay. Data were analyzed with 2-way ANOVA with location and substrate the two main, fixed factors.

RESULTS

Minimum Fragment Size Bioassays

Invasive Caulerpa fragments from Lake Conjola did not die immediately after cutting. In trial 1, all fragments were alive after 48 hours. By day 3, there was mortality with 2 and 4 mm stolon and frond fragments. Colorless rhizoids became visible on larger fragments of stolons and blades on day 4 and by day 5, there were green stolons starting to grow from a variety of locations along the length of some of the larger fragments. By the end of the 8 days, some larger fragments from Lake Conjola had both rhizoids and multiple stolons that had bifurcated (Fig. 1). These results were very similar to growth rates for fragments grown in compartmentalized plastic boxes at both field sites (unpublished data). In Lake Conjola trials 2 and 3, mortality of small fragments and new growth on larger fragments both started one day earlier, day 2 and day 3, respectively. Interestingly, the smallest fragments from the native strain of C. taxifolia from Moreton Bay waters were not nearly as successful as the invasive strain from Lake Conjola. Many 2 mm blade and stolon fragments were dead within 24 hr. However, new growth was seen on day 3 in trial 1, day 2 on one 20 mm stolon in trial 2, and on day 4 in trial 3. The minimum size from stolon and blade fragment survival and new growth was surprisingly similar for the native versus invasive strains (Fig. 1). For blades at both sites, 4 mm fragment length was the minimum for success in 2 of the 3 trials with 6 mm needed for success in the third trial. With stolons, the minimum length for Lake Conjola fragments was 15 mm in two of the three trials, with the largest size tested (20 mm) needed in the third trial. At Moreton Bay, 20 mm of stolon biomass was needed in all three trials.

Fragment Creation in the Field

Both abiotic and biotic sources can create fragments of Caulerpa. At Lake Conjola, wind speeds reached a maximum of 16.6 km/hr during our trials and the mean number of boats per hour passing directly past our site that created wakes was approximately 14 (Table 1). Boats were primarily small pleasure boats used for fishing or towing water skiers. A mean of 34 fragments was found along the shore of Lake Conjola and 66% of these were longer than 20 mm. This compares to a mean of 20 fragments at Moreton Bay, with over 99% over 20 cm in length. In Moreton Bay, the mean maximum wind speed was 17.3 kph, which was higher than the highest wind speed recorded in Lake Conjola (16.6 kph, Table 1). However, the mean number of boats at Moreton Bay was over 50% lower (Table 1). Boating traffic in these shallow Queensland waterways was primarily large sailboats, small fishing boats and ferries. Only on one weekend was the boat numbers substantially higher (24 boats/hr) and that was the result of a weekend fishing tournament. Our data show that fragments are regularly being
created in both places that are large enough to be successful. Additionally, there may be
more fragments created in Lake Conjola from boating while winds in Moreton Bay may
be the primary source of fragmentation.

**Fragment Retention Trials**

The fragment retention trials showed that some small mimic fragments are
regularly retained in areas with *Caulerpa* and seagrass long enough for attachment
rhizoids/rhizomes to be produced (Figure 2). In all trials, retention was highest in the
dense *Caulerpa* beds, intermediate in the low density *Caulerpa* and *Zostera* beds, and
mostly absent in the bare sediment patches. However, in one Lake Conjola trial, one 20
mm fragment was retained for 4 days in the bare zone. This was the result of the
fragment being partially buried (about 50% covered) in the sediment by a burrowing
polychaete. For the fragments that we were able to track after they dispersed out of their
quadrat, the largest dispersal distance we were able to record in Lake Conjola was 625
cm for a 20 mm mimic fragment and 1067 cm for a 40 mm fragment. In Moreton Bay,
the longest measured dispersal was 733 cm for a 20 mm fragment and 765 cm for a 40
mm fragment. Many additional fragments were not recovered and likely traveled much
greater distances.

**DISCUSSION**

In Australia, both native and invasive *Caulerpa taxifolia* were equally very
successful at vegetative fragmentation. These results document that blade fragments as
small as 4 mm can be successful. Stolon-only fragments required significantly more
mass (15 – 20 mm) (Fig. 1). This small size will put a huge burden on those tasked with
monitoring and eradication, as 4 mm fragments will likely be overlooked. Currently the
fake *C. taxifolia* used in California to test the efficacy of the monitoring after all *C.
taxifolia* had been eradicated used mimics were significantly greater than 20 mm in
length.

This small size for success also suggests that boaters and other water users must
be restricted from areas when new infestations occur. In the Mediterranean Sea,
*Caulerpa taxifolia* – aquarium strain was concentrated in zones with extensive
development (Madl and Yip 2005) and it has been documented that humans create
fragments via boating and other water-related activities (West et al. 2007). Correlative
evidence was found in the Mediterranean with fragments of *C. taxifolia* found where
boats are commonly moored (Relini et al. 2000) and most new outbreaks appeared in
areas of high boating activity (Meinesz et al. 1993; Meinesz 1997). West et al. (2006)
determined that fragments of *C. taxifolia* greater than 20 mm were created by all anchor
types tested. Overall, 82% of anchors lowered into *C. taxifolia* beds created fragments.
The biomass removed by a single anchor was as high as 49 g dry weight (West et al.
2007). Materials that attached the anchor to the boat created less fragment biomass
overall and chain attachments removed larger clumps than rope attachments (96% chains
versus 4% ropes). West et al. (2007) also suggest that boaters may be more likely to
discard larger, more obvious clumps of *C. taxifolia* from anchors or attachments, while
smaller fragments may be overlooked. Our results suggest that even the smallest
fragments must create concern.

Days with the largest numbers of generated fragments in Lake Conjola (207) and
Moreton Bay (60) appear to be directly related to human activities. At the former site, a
recreational boat had pulled ashore directly over the *Caulerpa* beds for a picnic
immediately prior to the fragment census (pers. obs.). In Moreton Bay, a fishing
tournament that brought in many additional wake-producing boats was the day we
collected the largest number of fragments (Table 1). The second-largest fragment
producing day in Moreton Bay was immediately after a pair of fishermen motored over
the *Caulerpa* bed to collect bait in the intertidal zone.

Wright and Davis (2006) were the first to experimentally determine that stolon
growth and fragment success were linked in *C. taxifolia*. They found that fragment
recruitment was enhanced when stolons were present compared to when they were absent
and as the abundance of *C. taxifolia* overall increased. However, seeding quadrats with
fragments had no effect on its biomass over six months (Wright and Davis 2006). By
comparing core samples from invasive locations and Moreton Bay, Wright (2005) found
significantly higher densities of fragmented fronds (as high as 6000/m²) and thus more
asexual reproduction via fragmentation in the native rather than at the invasive locations.
Additionally the presence of stolons increased the number of fragments that recruited to
the area (Wright and Davis 2006). However, we found that when areas with similar
starting densities of 3-D structures (*Zostera* or *Caulerpa* blades) are considered for
fragment retention, the results were similar for Moreton Bay and Lake Conjola (Fig. 2).

Smith and Walters (1999) found that fronds of *C. taxifolia* from native Hawaiian
populations readily produced new attachment rhizoids/rhizome with a minimum size of
10 mm in 14-day trials. However, the only smaller size class tested was 5 mm. None of
the stolon fragments from Hawaii produced new growth at any of the tested sizes (length:
5, 10, 15, 20 mm). Like our trials, new rhizome growth occurred at the wound sites,
undamaged growing edges and along branchlets. Rhizoids were only produced at the cut
in all cases. We stopped our trials at day 8, in part because some rhizomes had become
so large that they were growing out of their wells. Smith and Walters (1999) also
determined the forces required to create fragments of *C. taxifolia* using a puncturometer
(Pennings and Paul 1992). Forces needed were significantly less for frond versus stolons
(Smith and Walters 1999). All averaged less than 0.55 MPa (Smith and Walters 1999).
This is similar to other macroalgae, such as *Acanthophora spicifera*, that vegetatively
fragment (Kilar and McLachlan 1986). Although this value was not calculated for native
versus invasive *C. taxifolia* in Australia, over 75% of the fragments collected in both
locations were blade tips with no attached stolon biomass. Stolon-only fragments were
rare, accounting for less than 10% of total fragments found.

The saltwater aquarium industry is a huge business (e.g. Padilla and Williams
2004). While most of the economic and ecological impacts of this business can be
enumerated (e.g. Walters et al. 2006; Zaleski et al. 2006), one critical aspect that
effectively cannot be quantified is the number of accidental and purposeful releases of
organisms from aquaria into coastal waterways. In spite of this missing information, some of the most harmful invasive species that have become established in the United States waters are presumed to be the result of aquarium releases (e.g. Padilla and Williams 2004; Semmens et al. 2004; Ruiz-Carus et al. 2006). The origin of the US and Australian invasions will never be known, but the similarity to the Mediterranean invasion lends support to aquarium releases (Stam et al. 2006). In spite of its invasive reputation, many members of the genus Caulerpa remain extremely popular with aquarium hobbyists (Walters et al. 2006; Zaleski and Murray 2006). In three 2006 publications, the popularity and ease with which Caulerpa is dispersed within United States boundaries via the aquarium industry was documented. Zaleski and Murray (2006) focused on availability of the genus Caulerpa in retail shops in southern California immediately after the first California invasion was reported. They found no seaweed for sale in large corporate/franchise pet stores, so they focused on independent, non-franchise stores that specialized in ornamental aquariums for hobbyists. 10 species of Caulerpa were for sale in 52% of 50 stores visited between November 2000 and August 2001. Fourteen percent had C. taxifolia. In 2006-2007, Diaz and Murray (pers. com.) resurveyed these shops. 44 were still in business. In spite of the California code currently banning 9 species of Caulerpa, including C. taxifolia, and all the publicity associated with the 2 California invasions, 52% of the shops still sold at least one species of Caulerpa and 4 had C. taxifolia. Two other banned species, C. racemosa and feathery C. sertularioides, were also found (Diaz and Murray unpublished data).

Thirteen species of Caulerpa are widely sold through internet outlets (Walters et al. 2006, Zaleski and Murray 2006; Stam et al. 2006). Dealing with 30 internet commercial retailers and 60 internet auction sites (eBay), Walters et al. (2006) were able to make online purchases of Caulerpa from 25 states and Great Britain. Confirmed by DNA sequencing, this included 12 species of Caulerpa, including C. taxifolia and C. racemosa. Caulerpa taxifolia was purchased only once and was listed as “green feather Caulerpa”. It was shipped from a southern California internet retailer in November 2004. It turned out to be a specimen from the Caribbean based on the DNA sequence analysis (Stam et al. 2006). Now knowing that such small fragments of C. taxifolia can potentially survive if released by misguided hobbyists adds urgency to outreach campaigns for hobbyists as the most cost-effective management strategy in the marine environment is to minimize the introduction of C. taxifolia.

Information on minimum fragment size is also critical for individuals tasked with removing C. taxifolia infestations. Although harvesting by hand or with a suction pump were rejected early on in the Mediterranean, it seems to be considered as a potential eradication alternative every time a new infestation is documented. Hopefully, these strategies will no longer be considered and other techniques with greater potential will be pursued, including covering C. taxifolia beds with black tarp or other materials that completely prevent light penetration (Anderson 2005), chlorine (Williams and Schroeder 2004), temperature shock (Williams and Schroeder 2004) and coarse sea salt (Glasby et al. 2005). Two biological control agents, the Mediterranean sea slugs Oxynoe olivacea and Lobiger serradifalci, have been tested in aquariums and in the open ocean as potential biological control agents of C. taxifolia (Thibaut and Meinesz 2000). In lab
studies, the Mediterranean sea slug *Lobiger serratifalci* was shown to create viable fragments of *C. taxifolia* when feeding (Zuljevic et al. 2001). When feeding, *Oxynoe olivacea* did not generate new fragments.

**LITERATURE CITED**


Table 1. All data are presented as mean ± SE followed by the range. N = 10 in Lake Conjola and N = 14 in Moreton Bay.

<table>
<thead>
<tr>
<th></th>
<th>Lake Conjola</th>
<th>Moreton Bay</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of fragments</td>
<td>34.0 ± 19.8 (1 – 207)</td>
<td>19.7 ± 4.4 (4 – 60)</td>
</tr>
<tr>
<td>% fragments greater than 20 mm</td>
<td>66.1 ± 8.6 (0 – 100)</td>
<td>99.2 ± 0.6 (93 -100)</td>
</tr>
<tr>
<td>% fragments less than 10 mm</td>
<td>2.2 ± 1.4 (0 – 13.7)</td>
<td>0.1 ± 0.1 (0 – 1.7)</td>
</tr>
<tr>
<td>Wind speed (km/h)</td>
<td>9.8 ± 1.6 (3.3 - 16.6)</td>
<td>17.3 ± 2.0 (5.6-41.1)</td>
</tr>
<tr>
<td>Salinity (ppt)</td>
<td>34.4 ± 0.6 (30 – 35)</td>
<td>34.8 ± 0.1 (34 – 35)</td>
</tr>
<tr>
<td>Temperature (C)</td>
<td>24.0 ± 0.8 (20 – 27)</td>
<td>26.5 ± 0.3 (23 – 29)</td>
</tr>
<tr>
<td>Number boats/hr</td>
<td>13.9 ± 2.3 (2 – 32)</td>
<td>5.9 ± 1.0 (1 – 24)</td>
</tr>
</tbody>
</table>
Figure 1: Minimum Fragment Size for New Growth

LC = Lake Conjola trials; MB = Moreton Bay trials.
Figure 2: Fragment Retention

- Lake Conjola
- Moreton Bay
Appendix 8.

Distribution, Habitat Utilization, and Reproductive Patterns in *Caulacanthus ustulatus* (Caulacanthaceae, Gigartinales), a Newly Established Seaweed on Southern California Shores

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INTRODUCTION

Marine communities around the world are experiencing shifts in community composition due in large part to human-mediated disturbance (Fields et al 1993, Harley et al 2006). Pollution, coastline modification, increased global warming, collecting and trampling by seashore visitors have all resulted in dramatic changes in species composition and thallus size structure over the last several decades (Murray et al 1999). Southern California, in particular, has experienced large population increases, which have put pressure on local marine communities (Murray et al 1999). Since the 1950s researchers have followed intertidal algal community composition as a means of detecting human-induced changes on marine ecosystems (Dawson 1959, Dawson 1965, Widdowson 1971, Littler & Murray 1975, Thom & Widdowson 1978, Murray et al 2001). In areas where pollution is high, researchers have found that large fleshy algae have decreased in percent cover, while more resistant crusts, coralline algae, and turf species have increased (Murray & Littler 1984). High human visitation has been correlated with decreases in the size structures of seaweed populations (Murray et al 2001) and is linked to shifts in species composition (Bullard 2005). Furthermore, human activities such as boating and aquarium keeping have resulted in increases in the presence of introduced species in southern California waters (Frisch 2003). In 1970, *Sargassum muticum* was recorded on Santa Catalina Island and by the following year could be found throughout Orange and San Diego Counties (Abbott & Hollenberg 1976). Recently, reports of species previously unknown or ignored in southern California have increased with the spottings of *Undaria pinnatifida*, *Lomentaria hakodatensis*, *Caulerpa taxifolia*, and *Caulacanthus ustulatus*, which have made their way to local waters within the last decade (Miller 2004). *Caulacanthus ustulatus*, a cryptogenic red seaweed, was first recorded at Corona del Mar, Orange County, in 1999 (Goodson 2003). Researchers saw an increase in the cover of this species (Murray pers comm.), but little was known about the ecology and extent of its distribution on southern California shores. This study examines the current distribution and abundance of *Caulacanthus* at both spatial and temporal scales. Additionally, in order to understand how southern California populations of *Caulacanthus* reproduce and disperse, we examined the phenology of this species.
MATERIALS & METHODS

World distribution

The worldwide distribution of *Caulacanthus ustulatus* was compiled from 2003-2007 using 152 herbarium specimens and 123 published literature references. Information on the 152 herbarium specimens was collected from the herbaria at UC Berkeley (UC), University of Michigan (MICH), and the Smithsonian Institution (SHUS). Literature references were collected through the use of internet searches, library search engines, and perusing the bibliographies of key papers on seaweed distributions. Data gathered from the herbarium collections and literature were used to plot *Caulacanthus* occurrences in order to provide an up-to-date map of the geographic distribution of this species. Information on introduced populations and the recorded reproduction condition of natural populations was also collected.

Southern California Distribution and Abundance

To determine the distribution of *Caulacanthus* in southern California, rapid-assessment surveys were conducted from November 2004 to June 2007 from Santa Barbara County to San Diego County, California. Thirty rocky intertidal sites, five from each of six southern California counties, were randomly chosen from 72 sites, which have historical floral information (Dawson 1959, Dawson 1965, Widdowson 1974, Thom 1976, Thom & Widdowson 1978). Several of these sites continue to be monitored by the Multi-agency Rocky Intertidal Network (MARINe). Sites were searched for 20-30 min, if *Caulacanthus* was present, its cover was estimated over 100 m of coastline where the species was most abundant. Cover was estimated in 20 m sections using a modified Braun-Blanquet scale (0 = absent, 1 = present or >1%, 2 =1-5%, 3 = 5-10%, 4 = 10-25%, 5 = 25-50 %, 6 = <50%). These 20-m estimates were then averaged to determine the overall site rank in terms of *C. ustulatus* abundance. Voucher specimens were collected for later deposition at the UC Herbarium at Berkeley and for additional phenological and morphological examination.

Local Site Abundance and Distribution

To determine local site abundance and distribution we calculated the percent cover of *Caulacanthus* along permanent transects (31-42 m in length) from January 2003 to June 2006 at rocky intertidal sites at Corona del Mar and Dana Point in Orange County. Macrophyte cover and habitat utilization were determined using a point contact methodology at 10 cm intervals along each transect line. Species cover was determined by identifying all algal species to the lowest possible taxon for each contact point. Habitat utilization was determined by identifying the substratum utilized by *Caulacanthus*, including other living species. Tidal heights were taken at 1 m intervals along each line in order to plot species cover as a function of tidal height. The tidal interval means were then averaged to estimate overall site abundance. To examine habitat utilization available substratum and *Caulacanthus* utilization were analyzed using
an electivity index (Krebs 1989). This ensured that we accounted for the availability of a particular substratum type.

\[
\text{Electivity Index} = \frac{(P_{\text{use}} - P_{\text{available}})}{(P_{\text{use}} + P_{\text{available}})}
\]

**Morphology and Reproduction**

Morphologies of specimens collected from five individuals from each of 15 sites ranging from Rueben Tarte Park, Washington, USA to San Quintin, Baja California, Mexico, were compared using three morphological characteristics. Individuals were chosen randomly along a 100 m of coastline and preserved in 4 % formalin seawater for later examination under a stereomicroscope. For each thallus, measurements were taken on five randomly chosen sections. On each section the following measurements were made: the number of branches within a 1 cm section of thallus, branching distance, and thallus diameter. Measurements were compared with data from the scientific literature using principal components analysis (PCA) to determine which of the measured characteristics contributed to the overall similarity/differences between geographic areas.

Seasonal variation in the phenology of *Caulacanthus ustulatus* was determined from February 2006 to February 2007 by examining specimens collected monthly from Crystal Cove and Dana Point in Orange County, California. Twenty-five specimens were randomly collected along five permanent transect lines established at each site. Samples were transported to the lab and preserved in 4 % formalin seawater until examination. For each individual, 1 g (wet weight) was examined for reproductive material using a stereomicroscope. Tetrasporophytes, carposporophytes, and gametophytes were identified when present using descriptions from Choi et al (2001). Average monthly temperatures from NOAA offshore buoys were compared with the reproductive results to determine if temperature could be correlated with the seasonal development of reproductive structures.

**RESULTS**

**World distribution**

*Caulacanthus ustulatus* can be found everywhere from boreal regions to the tropics; in mangroves, brackish waters, and coastal intertidal habitats. The species is located within nineteen biogeographic regions (adopted by the Smithsonian herbarium): Japan, Pacific Ocean Terrestrial, North Pacific Boreal, North Pacific Temperate, Gulf of California, Central American Terrestrial, Southeast Pacific Temperate, Fuegian, Tropical West Atlantic, Eastern South America, West Indies Terrestrial, Boreale, Lusitania, Mediterranean, Tropical East Atlantic, Cape, Indo-west Pacific, Indian Ocean Terrestrial, an New Zealand. Introduced populations have been recorded in Roscoff, France (Rueness & Rueness 2000), Prince Willliam Sound, Alaska (Ruiz et al 2006), and Neeltje Jans, Netherlands (Stegenga et al 2006). Early reports of *Caulacanthus* in the Eastern Pacific describe a disjunct distribution with *Caulacanthus* populations reported in Washington and British Columbia and in Baja California (Dawson 1961, Dawson 1966),
but with no mention of records from Oregon or California before 1987. The first record for California came in 1987, when Dr. Chris Kjeldsen reported *Caulacanthus* in Tomales Bay, California (Gabrielson et al 2004). Then in 1999 the species was reported for the first time in southern California from Corona del Mar, Orange County (Goodson 2003). Since that time the species has spread to other localities in the area and into some isolated northern California locations.

The species exhibits a tri-phasic life-cycle and like many red algal species not all phases are displayed throughout the species range. Herbarium specimens and literature sources point to populations often consisting solely of vegetative thalli or with vegetative thalli and some tetrasporophytic material present. Carposporophytes and gametophytes appear to be found only in populations in the following biogeographic regions: Lusitania, Mediterranean, Cape, Indo-west Pacific, and New Zealand. In the Eastern North Pacific, the northern populations in Washington and British Columbia do not appear to be fertile, while material in Baja California contained tetrasporophytes.

**Southern California Distribution and Abundance**

Our surveys of 30 intertidal sites along with reports from other researchers showed that *Caulacanthus* is widespread along the southern California mainland from central Los Angeles County to San Diego Bay and on Anacapa and Santa Catalina Islands. Surveys from sites north of Paradise Cove in Los Angeles County to the Vandenberg Airforce Base in Santa Barbara County did not contain *Caulacanthus*. The next northern site on the California mainland where *Caulacanthus* appears is Hazards Canyon in Montana de Oro State Park in San Luis Obispo County.

**Local Site Abundance and Distribution**

*Caulacanthus* cover has been variable over the last four year ranging from a minimum intertidal cover of 2.2 % in the summer of 2006 to a maximum 9.8 % in the winter of 2003 at Corona del Mar and from a minimum of 7.3 % in the winter of 2003 to a maximum of 15.1 % in the summer of 2004 at Dana Point (Fig 1). While the cover at Corona del Mar, a high-use site, has seen decreases in cover over time; Dana Point, a low-use area, has seen higher cover in the later years of this study beginning in the summer of 2004. There does not appear to be a strong seasonal abundance signal at either site; however, Dana Point seems to show small winter decreases and summer increases. Examination of vertical distribution and microhabitat utilization show that *Caulacanthus* is more abundant in the mid-intertidal zone; within this zone the distribution differs slightly. At Corona del Mar, *Caulacanthus* is more often found from the +1 to +5 ft tidal range with relatively the same abundance across the interval and decreases significantly in the MLLW to +1 ft interval. At Dana Point, the species is distributed lower on the shore, from the +3 to +5 ft interval and the MLLW to +1 ft interval; the most utilized portion of the intertidal at Dana Point is the +1 to +3 ft tidal interval. At Dana Point, in the higher tidal intervals the available substratum is composed of large boulders that are most likely moved during heavy winter swells. Microhabitat data analyses revealed the high epiphytic tendency of this species. *Caulacanthus* was
found growing on a multitude of living substrata more often than on rock surfaces. The living substrata utilized by *Caulacanthus* fell into five main categories: articulated corallines, barnacles and mussels, *Silvetia* and large brown seaweeds, and crusts. Both sites were similar except for *Silvetia* and large brown seaweeds, which were absent or scarce at Corona del Mar. Based on electivity calculations, barnacles and mussels were utilized more than any other substratum group, followed by *Silvetia* & large browns (Dana Point only), turf forming species, crusts, and finally articulated corallines.

![Graph showing percent cover of Caulacanthus at Corona del Mar and Dana Point](image)

**Fig. 1.** *Caulacanthus* cover at Corona del Mar and Dana Point during winter (W) and summer (S) from 2003-2006.

**Morphology and Reproduction**

There are no results available at this time for the morphological portion of this study; this work remains in progress. All specimens are collected and are being examined. The reproductive portion of this study is also underway. Preliminary results, based on inspection of 300 samples from both Dana Point and Crystal Cove, reveal that only 7 specimens were reproductive – all tetrasporophytic; all remaining specimens were sterile. Three tetrasporophytes were found from Crystal Cove and four from Dana Point. Neither gametophyte nor carposporophyte material has been observed at either site.

**DISCUSSION**

Since its arrival 1999, *Caulacanthus* has spread along the southern California coast and become one of the major contributors to intertidal algal cover and primary production (Bullard 2005). Although, its origins are still uncertain, the historical disjunct distribution, the patchy spread of *Caulacanthus* along the California coast, its sudden increase in abundance, and the genetic alignment of southern California samples (Murray & Hommersand per comm.) with introduced specimens from Roscoff, France, and native Asia material strongly suggest that this species is an introduction. Further genetic work using microsatellites could resolve this question. Our microhabitat data show that *Caulacanthus* is spreading mostly through the mid-intertidal zone and will grow on almost any substratum (the species has even been found on the girdles of chitons). Lastly we conclude that the vast majority of *Caulacanthus* specimens in southern California are sterile with only a few being tetrasporophytic. This suggests that
vegetative fragmentation is the most likely mode of reproduction and dispersal for this species, which is in line with expectations for many introduced seaweeds.

**LITERATURE CITED**


Frisch SM (2003) Taxonomic diversity, geographic distribution, and commercial availability of aquarium-traded species of *Caulerpa* (Chlorophyta, Caulerpaceae) in southern California, USA. Calif State Univ, Fullerton MA Thesis


