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Hydrodynamic Regulation of Reproduction in Fucoid Algae: A Regional Model and Consequences for Population Structure

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Principal Investigator: Brawley, Susan H.
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Project Participants

Senior Personnel

Name: Brawley, Susan
Worked for more than 160 Hours: Yes
Contribution to Project:

Post-doc

Name: Coleman, Melinda
Worked for more than 160 Hours: Yes
Contribution to Project:
Ms. Coleman will complete her Ph.D. thesis with Dr. Tony Underwood at the University of Sydney in December, 2001, and will arrive in my lab in mid-January 2002 to begin her work on this project. Although the delay in her arrival caused some of the field work anticipated for Y1 to be postponed, her qualifications were so much higher than any other applicant that I decided to wait. Prof. Underwood described her as one of his best students (ever), a judgment supported by her transcripts, fellowships, and other letters of reference.

Graduate Student

Name: Muhlin, Jessica
Worked for more than 160 Hours: Yes
Contribution to Project:
Jessica Muhlin entered the University in September, 2001, as a M.S. student. She has helped with preparation of the field site at Schoodic Point, survey of other field sites, collection of samples and extraction of DNAs. We are now beginning AFLPs on these samples.

Name: Gordon, Richard
Worked for more than 160 Hours: Yes
Contribution to Project:
Finished M.S. work on effects of water motion on algal reproduction (studies of Alaria, Ulva, Chondrus, Porphyra, and Pseudonitzschia): his work on Pseudonitzschia was completed due to a small amount of support through this award.

Name: Koester, Julie
Worked for more than 160 Hours: Yes
Contribution to Project:
Helped with field work and related diatom studies.

Undergraduate Student

Technician, Programmer

Other Participant

Research Experience for Undergraduates

Organizational Partners

Other Collaborators or Contacts

Activities and Findings

Research and Education Activities:

This grant had three major objectives: 1) to describe gamete release in the rockweed Fucus vesiculosus L. with respect to coastal topography and create a predictive, regional model for gamete release, 2) to examine population genetic structure in this intertidal alga, and 3) to determine whether hybridization between F. vesiculosus and other fucoids is related to hydrodynamic-based aging of gametes due to lengthy inhibition of gamete release in stormy periods. I was unable to test objective 3 conclusively due to logistical constraints (unfavorable periods of stormy conditions) but objectives 1 and 2 were completed and led to additional work, as described below, to develop inexpensive GPS-reporting drifters and to examine related hydrodynamic effects upon the rockpool alga Fucus distichus.

Objective 1. We collected extensive data on gamete release and associated environmental conditions (irradiance levels, water motion) throughout the tidal cycle at four sites around Schoodic Point (two on each side of the point) throughout the autumns of 2002-2004. Sperm concentrations were determined using monoclonal antibodies; eggs were counted directly from concentrated plankton samples in and above the beds. We established 4 pumping stations to collect samples at 30 min intervals during high tide with 3 collection sites/pumping station in the fucoid bed; these were established using random numbers and a linear transect. My central hypothesis was falsified (i.e., that gamete release would occur at different times between sites on different sides of the coastal point), although the hydrodynamic situation usually followed that which I had predicted, making two sites (one side of the point) calm on days when the other two sites experienced high wave action. Gamete release in fucoids is triggered by a photosynthetic pathway (as previously shown by my laboratory), and in this study, we found that it requires a minimal period of about 2 hours of 100 Ámol photons m2 s (or higher) irradiance at the bed during high tide for gamete release to occur. Coastal fog often caused sites on the same side of Schoodic Point to have dramatically different irradiances so that gamete release would occur at one site but not the other, despite hydrodynamic conditions (Beaufort scale 0-1; also measured by clod cards with some Marsh-McBirney current meter calibrations) that were permissive for gamete release at both. A few days, especially in September, were calm and sunny at all sites; as expected, gamete release occurred at all sites on these days. Other days were cloudy or stormy at all sites and no gamete release occurred. These findings have resulted in tighter thresholds on predictions on when gamete release from fucoids can occur, and they are now being put into a larger framework of New England/Maritime archival data (especially from GoMOOS sensors) to make a regional model for gamete release by these algae. I expect this work to be completed by early 2007. As a result of this work, the reproductive ecology of fucoid algae will continue to be at the forefront of our understanding of how oceanographic and meteorological conditions affect the life histories and recruitment of marine species.

We explored the effects of water motion on gamete and zoospore release in other species (the kelp Alaria esculenta and the sea lettuce Ulva lactuca) for a comparison to fucoid algae, and found that higher levels of water motion enhance the release of reproductive propagules in U. lactuca and of zoospore release in Alaria under laboratory conditions, but inhibit sperm release in Alaria (Gordon & Brawley, 2004). Understanding the effect of water motion and genetic diversity on sexual reproduction in phytoplankton species is virtually unknown, and essential to understanding life histories/bloom dynamics in these species. This grant supported a small amount of preliminary study of sexual reproduction in the marine centric diatom Ditylum brightwellii (Koester et al., in prep).

Objective 2. I completed development of microsatellite markers for studies of population genetic structure in F. vesiculosus (see publications: Engel et al., 2003). Most of the 6 loci defined as polymorphic in F. vesiculosus are also polymorphic in other fucoids (Coleman & Brawley, 2005a, b) and are of general utility to other marine biologists. Using the microsatellite markers, we tested whether population genetic structure in Fucus vesiculosus follows an isolation by distance model or a topographically-related model (Objective 1). We found that neither model applies. Isolation by distance was not found at any scale in studies of 4 populations (two from each side of the coastal point) over two points (Scoodic and Pemaquid Points in Maine) that are about 200 km apart. The sites at Schoodic Point were the same ones at which gamete release was monitored in Objective 1. We found a high degree of population genetic structure (on a scale of a meter) throughout the study area, with some sites from Pemaquid and Schoodic being more similar to each other than to their nearest neighbors (Muhlin et al. 2005, in prep.). This strongly suggested that population structure might be determined not by dispersal of gametes or zygotes but by rafting adults that are dispersed following storms to new locations, where they release gametes and interbreed with attached algae. We tested this hypothesis in two ways: 1) releases of labeled oranges (fruit) at each site on multiple days (100 oranges/site; 800 oranges/day), and 2) by release of a newly-developed, inexpensive GPS drifter that continuously reports its location from several of our study sites (Stessel et al., in prep; Muhlin et al., in prep). The oranges moved around the points in different directions on different days and reached shore, showing that rafting of adults could create the heterogeneity observed with the microsatellite markers. Continuous tracks supporting this observation were obtained with the drifter. There are

virtually no descriptions in the literature of dispersal affected by local, nearshore currents; this work fills that gap. We expect the technical development of an inexpensive drifter (i.e., most parts from Home Depot and total cost of about $500) to be useful to other marine biologists. Although biologists in the past speculated that rafts of drifting algae have been important in recolonization of denuded shores (e.g., after the Last Glacial Maximum), our correlated population genetic and oceanographic work shows that these effects are important over scales of 100s of km on short and long temporal scales. Because many other organisms occur on fucoids as epiphytes or associated microfauna, our studies on rafting and population structure will inform similar studies by other biologists on other marine organisms.

Schoodic Point, one of the major study areas for Objectives 1-3, lies largely within Acadia National Park, and our work there required permits from the National Park Service. The work within Objective 2 is particularly useful to the NPS, because they are using it to predict the effect that a toxic spill (e.g., an oil spill) would have on the marine biota within ANP (Manski, pers. comm.). We also engaged the Friends of Schoodic in release and recapture of marked oranges.

In companion population genetic studies of Fucus spiralis and F. distichus, we also found a lack of isolation by distance over the scale of Schoodic and Pemaquid Points (Coleman & Brawley, 2005a) in F. spiralis and F. distichus. The population genetic structure of F. distichus is not as inbred as might be expected for a high intertidal rock pool species, and we suggested that its reproductive seasonality (winter) is an evolutionary adaptation to prevent inbreeding, because zygotes have delayed attachment at low water temperatures and can be dispersed to other rockpools (Coleman & Brawley, 2005b). Further, speciation in the Fucus distichus complex may be inhibited by annual variations in air/water temperature, based upon our examination of climate and herbarium records over the last 100 years (Coleman & Brawley, 2005c).

Because we did not find isolation by distance (a common population genetic model) at the scale of the Maine shore in F. vesiculosus, we decided to study its population genetics over the larger regional scale for which we are creating a regional gamete release model (Objective 1). There is isolation by distance and fixation of some alleles over a North Carolina to northern Nova Scotian scale in this species (Muhlin et al., in prep.).

Findings:

Major Findings

ò Gamete release is temporally and spatially decoupled at small geographic scales in coastal populations of the abundant, intertidal alga Fucus vesiculosus due to significant variations in irradiance and wave action at these scales. Thus significant gamete release can occur at a site that is only a few km from another site at which gamete release is completely inhibited on that day. Gamete release is sometimes, but frequently not, related to coastal topography (i.e., the hypothesis that sites on the same side of a point would release gametes simultaneously and at a different time from sites on the other side of the point was rejected).
ò There was high genetic structure but no isolation by distance across several 100 km of Maine shore; this suggested that genetic structure is related to dispersal of reproductively mature and functional adult plants in storm-generated rafts that come ashore to interbreed with attached plants.
ò Nearshore conditions (currents, wind direction) vary to dramatically change dispersal trajectories of intertidal rafts of fucoids on the New England coast, as demonstrated inexpensively by large releases of marked oranges, and at a smaller scale by use of a newly designed nearshore GPS drifter. These results provide a physical model for understanding population structure in marine organisms subject to dispersal in floating algal rafts when isolation by distance is absent.
ò We found that water motion also affects gamete release in other algae, but it stimulates rather than inhibits gamete release in Ulva lactuca (a green alga) and also stimulates release of zoospores in Ulva and the kelp Alaria, while inhibiting sperm release in Alaria.

Training and Development:

Development of Human Resources. This grant supported the postdoctoral training of Dr. Melinda Coleman who successfully competed on its basis for a Young Australian Career Award (2005) and is now an Assistant Professor at the University of Adelaide. Ms. Jessica Muhlin is a Ph.D. Candidate supported by the grant, and she will receive her Ph.D. in May 2007 (all research is completed; she is now writing papers). Mr. Richard Gordon (M.S., 2003)'s research was supported in part by this grant, and he is now employed at Saigene in Seattle, WA. Mr. David Olson and Mr. Jeremy Winn did REU internships on the grant, and both are now enrolled as graduate students in Marine Science at the University of Maine. We involved three classes of fifth graders in Bradley, Milford, and South Bristol, Maine, and their teachers in the studies of nearshore dispersal using orange releases in autumn 2005. They also studied the fucoid life history and released gametes and fertilized eggs under Ms. Muhlin's direction. About 30 other adult volunteers in the Friends of Schoodic participated in the oranges' project.

Outreach Activities:

Jessie Muhlin used material she has learned on the fucoid system, Atlantic marine biogeography, environmental monitoring etc. in weekly

lessons in a marine biology class at Orono High School in 2004. She was supported by a NSF GK-12 fellowship, but her activities and base of knowledge for outreach in her assigned classes were from her research work on this grant and in associated classes.

I took student field trips to Schoodic Point to my field sites and talked to students about the importance of algae as model systems for understanding general principles of marine science; I did this for 150 middle school students in each year of the grant.

We involved a large number of volunteers (3 fifth grade classes in Maine, their teachers, some parents; 30 other adults in the Friends of Schoodic (a support group for Acadia National Park) in key field work related to the dispersal studies in 2005. They helped to release batches of oranges and then did field walks to try to recover them over the next few weeks. Before beginning this work with us, they heard seminars from Brawley or Muhlin about the larger project and its goals and learned to identify fucoid algae and release their gametes, including viewing gametes, zygotes and embryos at the microscope.

Personnel of Acadia National Park (rangers) have worked with us to use our data set to predict effects of toxic spills, oil spills, etc. on the marine biota of ANP. They previously did not have an adequate understanding of very nearshore currents to do so.

Newspaper and magazine stories on our work (i.e., in the Bangor Daily, on Maine Public Radio, and in Downeast Magazine) found their way to an artist who is a former Mainer living in Spain. She wrote to Ms. Muhlin to request that they do a joint art/science project by putting words on the oranges released by the 5th graders in fall 2005. The words were from local history, the biology of fucoids, etc. As oranges were found, the words were recorded in order and became 'found poetry'. Students have now written poems using the found words. The artist and Ms. Muhlin are hoping that a Maine museum will display the resulting work. This is an outstanding example of integrated learning for K-12 students.

Journal Publications

Engel, C. R., S. H. Brawley, K. J. Edwards & E. Serrão., "Isolation and cross-species amplification of microsatellite loci from the fucoid seaweeds Fucus vesiculosus, F. serratus, and Ascophyllum nodosum.", Molec. Ecol. Notes, p. 180, vol. 3, (2003). Published

Gordon, R. & S. H. Brawley, "Effects of water motion on propagule release from algae with complex live histories.", Mar. Biol., p. 21, vol. 145, (2004). Published

Coleman, M. & S. H. Brawley, "Are life history characteristics good predictors of genetic diversity and structure? A case study of the intertidal alga Fucus spiralis (Heterokontophyta: Phaeophyceae)", J. Phycol., p. 753, vol. 41, (2005). Published

Coleman, M. & S. H. Brawley., "Spatial and temporal variability in dispersal and population genetic structure of a rockpool alga.", Mar. Ecol. Prog. Ser., p. 63, vol. 300, (2005). Published

Coleman, M. & S. H. Brawley, "Variability in temperature and historical patterns in reproduction in the Fucus distichus complex. Implications for speciation and the collection of herbarium specimens.", J. Phycol., p. 1110, vol. 41, (2005). Published

Koester, J., L. Karp-Boss, D. Mann & S. H. Brawley, "Sexual reproduction in the marine centric diatom Ditylum brightwellii.", Eur. J. Phycol., p. , vol. , (2006). Will be submitted by 4/06

Muhlin, J.F., C.R. Engel, S.H. Brawley, "The influence of coastal topography and circulation patterns in structuring populations of Fucus vesiculosus L.", Evolution, p. , vol. , (2007). Will be submitted by 4/06

Stessel, R., J.F. Muhlin, J.F., and R.A. Weatherbee, "Development and application of a low-cost, nearshore drifter- technical paper.", Limnol & Oceanogr, p. , vol. , ( ). To be submitted by 8/06

Muhlin, J.F., M.A. Coleman, and S.H. Brawley., "Reproductive timing in the intertidal zone: a regional model of reproduction for Fucus vesiculosus", Mar. Ecol. Prog. Ser., p. , vol. , ( ). To be submitted by 12/06

Books or Other One-time Publications

Web/Internet Site

Other Specific Products

Product Type:

Physical collection (samples, etc.)

Product Description:

About 700 herbarium specimens of fucoid algae.

Sharing Information:

Most of these will be deposited into the University Herbarium of the University of Maine

Contributions

Contributions within Discipline:

There are many marine biologists in the US and elsewhere who are working with fucoid algae who will be benefited by my development of 9 microsatellite loci for work with most species of Fucus; two of these loci are polymorphic in Ascophyllum, thus these markers will be useful to workers needing markers for any member of the Fucales. Sequences were deposited at GenBank and published in Molecular Ecology (see Publications).

The work completed in this grant maintains fucoid algae as (in my opinion) the marine system we understand best from the viewpoint of reproductive ecology and, now, how dispersal and oceanographic forces interplay to produce the species' population structure, which we've now described at several scales (meters, km, 100s-1000s of km).

Contributions to Other Disciplines:

The microsatellite loci contribute to studies independent of our own by scientists in the US and Europe who are primarily systematists and phylogeographers; they are interested in understanding population genetics as part of their own studies.

The project has become unexpectedly interdisciplinary (encompassing the humanities) as a Spanish artist became involved to create a science/art/poetry project on dispersal.

Acadia National Park values the data of the project because it is a baseline of information on a major species within the park and the dispersal data help them predict the results of potential toxic spills nearshore.

Contributions to Human Resource Development:

A postdoctoral fellow, two graduate students, and two undergraduates were trained through the grant. The undergraduates were involved in a large logistical operation in the field (gamete collection) and learned important skills related to independent research and teamwork. The postdoctoral fellow and graduate students learned to do fluorescence microscopy and immunolocalizations, DNA extractions and microsatellite-based genotyping, and environmental monitoring in the field. One of the graduate students (Ms. Jessica Muhlin) co-developed an inexpensive GPS drifter with two physical oceanographers at the University of Maine and has independently made significant contributions to uniting physical and biological oceanography with marine biology to study dispersal and recruitment in marine species. Further, about 1000 K-12 students benefited from the project via activities, lectures, and (for about 80 of these students), key project work on dispersal of marine species. Through newspaper and magazine reports, the public at large has a better appreciation for the biology of a major component of the North American intertidal zone.

Contributions to Resources for Research and Education:

Reported elsewhere.

Contributions Beyond Science and Engineering:

The integration of science, art, and poetry that was an unexpected outcome of outreach components of the project caught the imagination of a wide segment of the Maine public.

Categories for which nothing is reported:

Organizational Partners

Any Book

Any Web/Internet Site