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The Fourth North American Echinoderm Conference, 22-26 August 2001

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DEDICATED SECTION

THE FOURTH NORTH AMERICAN ECHINODERM CONFERENCE 22-26 AUGUST 2001

Friends of Echinoderms Share Their Research and Renew Their Enthusiasm

JOHN H. DEARBORN

As demonstrated by the enthusiasm of the participants and the diversity and high quality of oral and poster presentations, echinoderms continue to intrigue, delight, and cast their mysterious appeal over invertebrate zoologists both young and old. Seventy-four specialists from 18 states, the District of Columbia, and six foreign countries (Austria, Belgium, Canada, Israel, South Africa, and the United Kingdom) met together 22-26 Aug. 2001 for the Fourth North American Echinoderm Conference. Many participants traveled with family members, so the total number of people involved was considerably higher. The meeting turned out to be a wonderful blend of formal presentations, informal discussions, and debates and social gatherings, including outdoor picnics, a lobster and clam bake, and a delightful early evening cruise along the central Maine coast. The conference was held at the University of Maine's Darling Marine Center (DMC) in Walpole, near Damariscotta, Maine. The Organizing Committee consisted of Emma Creaser, Unity College; Kevin Eckelbarger, Director of the DMC; Isidro Bosch, SUNY Geneseo, and John M. Lawrence, University of South Florida. Our local hosts and organizers, in addition to Creaser and Eckelbarger, were DMC staffers Linda Healy (Science Writer and Events Coordinator) and Tim Miller (Laboratory Manager). They and other DMC employees, especially Susan Elwell, Irene Leeman, and Karen Templeton, worked together efficiently and tirelessly to make the conference a roaring success. I thank them all for a truly exciting and stimulating scientific meeting and a memorable opportunity to interact with colleagues in a spectacular natural setting. Learning about echinoderms in a beautiful conference center overlooking the Damariscotta River is not a difficult way to spend 4 days!

DEDICATION

This conference was dedicated to Larry McEdward, who died 2 July 2001. Larry was an intellectual powerhouse who enjoyed an international reputation as an authority on invertebrate reproduction, especially the comparative morphology, growth, and energetics of echinoderm larvae and juveniles. He published many papers on these general topics, both specific research contributions and review articles, often in collaboration with colleagues and students, with special attention to asteroids and echinoids. He was equally at home in the laboratory or in the field. Collecting locations in Puget Sound and Florida were special. Larry was a person of diverse interests, both as a scientist and in his outside pursuits. His passion for off-road mountain bikes was legendary. The marine biology community has lost a dynamic colleague. Larry will be remembered with respect and admiration.

CONFERENCE PROCEEDINGS

During the conference, a total of 61 presentations were made consisting of a report on the history of the North American Echinoderm Conferences, three plenary talks, and 56 research presentations (41 oral reports and 15 posters). On Wednesday evening, 22 Aug., Kevin Eckelbarger welcomed the registered participants and others and gave a brief history of the development of the center and a description of the present status of the teaching, research, and public service missions and discussed some of the plans for future development. The next morning, John Lawrence began the session with a spirited review of previous NAEC meetings from tentative beginnings in 1972 at the Smithsonian Institution in Washington, DC, to the present. His personal enthusiasm for such meetings was clearly reflected by the participants. All seemed to agree

that informal meetings open to scientists interested in any aspect of echinoderm biology should continue at regular intervals and that such meetings were especially useful in providing opportunities for participation by graduate students, many of whom were in attendance.

Three plenary talks were given by me, Paul A. Tyler and Craig M. Young, and John S. Pearse. I discussed the echinoderm fauna of the Gulf of Maine and some concerns about the commercial exploitation of the green urchin *Strongylocentrotus droebachiensis* and the holothurian *Cucumaria frondosa*. A total of 95 species of echinoderms occur in the Gulf of Maine, including Georges Bank, between the intertidal zone and the outer edge of the continental shelf at 500 m. Asteroids are represented by the highest number of species (37) and crinoids are least represented (4 species). There are 30 species of ophiuroids in the region, 7 echinoids, and 17 holothurians. A comparison with the shallow-water echinoderms of the Florida Keys and Bermuda confirms the relatively low species diversity but high biomass of the Gulf of Maine fauna. At present, only *S. droebachiesis* and *C. frondosa* are exploited commercially. Although there has been a small green urchin fishery in the Gulf of Maine for many years, it was not until about 1987 that widespread commercial exploitation began. In that year, about 2 million pounds were taken, largely by scuba divers. Just 6 years later, in 1993, the catch reached a peak of about 41 million pounds harvested by various methods, including extensive dredging. By 2000, the harvest was down to about 9 million pounds, and the decline is likely to continue. The sea cucumber fishery is equally vulnerable. Over 3 million pounds were harvested in the Gulf of Maine in 1994. In 2000, 9.5 million pounds were taken. Although some state regulations are now in place, in the early years of commercial activity both the urchin and sea cucumber industries were completely unregulated. The harvesting of these species and the potential for exploitation of other echinoderms in the future raise a number of difficult and as yet unresolved issues. Many biologists and industry officials are now aware of the validity of an ecosystem approach to resource management but for a variety of complex reasons we still tend to regulate on an individual species basis. As new marine resources are identified and exploited it is very difficult to create reasonable state and federal regulations *before* the resource is overfished. Proper background information on which to base sound management decisions takes time to obtain, and ap-

propriate data are rarely available before overfishing occurs. Moreover, at present there are few long-term, quantitative studies available on the interactions between commercially harvested and noncommercial species of invertebrates, especially echinoderms. For most of the general public, environmental issues involve vertebrates, especially birds and mammals. There is little knowledge of marine invertebrates and their ecological interactions. Thus, there is little or no public advocacy for reasonable regulations based on sound ecological data.

Paul Tyler and Craig Young presented a thoughtful discussion about echinoderm larvae, which often disperse far and wide but may not settle in an area where they can survive. They used the expression "alien invaders" to describe the situation. Many deep-sea echinoids and ophiuroids produce larvae that settle over wide bathymetric zones, but the juveniles or adults ultimately survive only in narrow depth ranges. A central theme of their presentation was that some shallow-water echinoderms can tolerate to various degrees the temperatures and pressures in the deep sea and may be invading that habitat, yet the specific pathways by which such colonization could occur remain uncertain. They suggest that at the present time the cold isothermal water columns near the poles are the most likely routes, whereas during the Mesozoic and early Cenozoic one or more warm isothermal columns were the most likely routes. They emphasized that echinoderms provide useful models for investigations of the origin of the deep-sea fauna, both present and past.

In the third plenary session, John Pearse reviewed two major paradigms in marine biology and presented compelling evidence suggesting that both ideas need to be largely discarded or at least reevaluated. His work was based on detailed studies of two abundant Antarctic echinoderms, the asteroid *Odontaster validus* and the echinoid *Sterechinus newmayeri*. Orton's Rule states that temperature change regulates seasonal reproduction and that where there is no temperature change, reproduction should be continuous. Pearse showed that both these two Antarctic species have strongly seasonal reproduction in a region where the water temperature is always close to -1.8 C. Thorson's Rule can be stated in various ways but the underlying theme is that pelagic, planktotrophic development is the dominant form of reproduction in tropical and temperate marine environments and is rare in polar and deep seas. Again, Pearse found that his research on *O.*

validus and *S. neumayeri* revealed an opposite pattern. Both of these animals have pelagic, planktotrophic larvae. The implications of these relationships in reproductive biology were followed by a lucid review of temperature adaptation and rates of respiration, development, and growth in echinoderms in general and polar species in particular.

The 41 oral presentations and 15 posters covered a wide range of taxonomic groups and functional levels from molecules and cells to synecology and aquaculture. In the 56 reports, major groups were represented as follows: crinoids, 0; asteroids, 7 (12.2%); ophiuroids, 6 (10.5%); echinoids, 30 (52.6%); holothurians, 8 (14%); and general papers on more than 1 echinoderm group, 5 (10.5%). Clearly, echinoids were the most popular subjects: Their reproduction, larval development, metamorphosis, and juvenile survival were common themes. The increasing commercial exploitation of several species of echinoids and holothurians along most U.S. coastlines, despite decreases in the natural populations, has created new interest in echinoderm aquaculture. A number of the participants at this conference presented information related to this topic in one way or another (see Lawrence and Watts, this issue).

The Fourth North American Echinoderm Conference left all of us with enduring memories of intellectually stimulating presentations and discussions, the remarkable efforts of Emma Creaser, Kevin Eckelbarger, and his staff in providing for our every comfort in the beautiful setting of the Darling Marine Center, the Rich Mooi-designed t-shirts, and the opportunity to renew friendships with colleagues old and new. One must read carefully all the many abstracts in this issue to appreciate the application of current technologies to the study of echinoderms and the ingenuity and enthusiasm with which these investigations have been conducted. Because I am from the University of Maine, my opinion is not without bias, but I felt that this conference was just what such an event should be: informal, yet with rigorous, diverse, and up-to-the-minute presentations. The beautiful Darling Center location was a bonus. Echinoderms are a unique group of invertebrates and they will continue to confound us and provide many more questions to be addressed at future meetings.

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NAEC History and Commentary

JOHN M. LAWRENCE

Echinoderm researchers from around the world gathered at the Smithsonian Institution in Washington, DC, in 1972 for the first International Echinoderm Conference. Participants at this meeting recommended that the international meeting be held every 3 years and that regional meetings be held in the intervening years.

Although meetings have been held regularly in Europe since 1979, it was not until 1989 that the first North American Meeting was held as the Friends of Echinoderms at the Dauphin Island Sea Lab on the Alabama gulf coast. The meeting was organized by James McClintock, Stephen Watts, and Tom Hopkins. I remember very well talking with Tom Ebert and Malcolm Telford on the beach. Steve Stancyk and his crew of brittle star people were there.

The second Friends of Echinoderms meeting was in 1992 at the Harbor Branch Oceanographic Institution. It was organized by Craig Young, Sid Bosch, and myself. I brought a number of tins of canned sea urchin roe from

Chile, but there were not many takers. Sid was disgusted that I had not brought Chilean wine instead. Dan Blake commented to Fred Hotchkiss and me that he did not recognize 50% of the persons there. I told him that was because 50% were younger than 50.

Because some university administrators did not think a "Friends" meeting could have academic and scientific respectability, the title of the third meeting was changed to the North American Echinoderms Meeting. It was held in 1998 at the Wallops Island Marine Science Center in Virginia and was organized by Thomas Klinger. I was particularly impressed with the participation of many graduate students, such as Emily Knott, Anne Boettger, Kristina Wasson, Christopher Mah, Ana Christensen, Nature McGinn, and Sophie Hill. At the other end of the generation span, Robert Hill talked about degenerating cucumber walls, and John Ferguson discussed fluid balance. Rebecca Ferguson, John's wife, talked with Bob and found

she had been a student at the University of Maine when he was an instructor there.

Over the years, these meetings have served a useful purpose by allowing echinoderm biologists from a wide array of disciplines to come together in an informal way to become acquainted with each other and each other's work. The interaction between graduate stu-

dents and established investigators has been particularly valuable. The 2001 NAEC Conference will certainly continue this tradition.

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Papers on Sea Urchin Fisheries and Aquaculture at the NAEC 2001: A Perspective

JOHN M. LAWRENCE AND STEPHEN A. WATTS

The roe of sea urchins have been consumed by humans since prehistoric times. They have become an important component of the marine fisheries market in the past 20 years. Overfishing has depleted sea urchin populations, and interest in understanding the fished populations is increasing. Because fisheries cannot continue to meet market demand, interest in aquaculture of sea urchins is also increasing.

FISHERIES

The papers presented did not deal with fisheries directly, but with various aspects of the biology and ecology of sea urchins that have implications for fisheries. Several papers considered the important species *Strongylocentrotus droebachiensis*, which is fished in the northwestern Atlantic and northeastern Pacific Oceans. Vadas et al. reported quickly growing and slowly growing morphs in sympatric populations of *S. droebacheinsis*, the presence of which has implications for fisheries management. Patterns of spawning in populations in the Gulf of Maine over a 3-yr period consistently coincided with the first increase in phytoplankton concentrations (Seward et al.). Interannual variation in spawning was significant, possibly as a consequence of interannual variation in phytoplankton concentrations.

Fertilization in the field has become recognized as an important factor in fisheries management. Egg longevity can determine population density necessary for successful fertilization. Meidel and Yund found that 75% of the eggs of *S. droebachiensis* are fertilizable in the laboratory for 72 hr after spawning. They suspended eggs in the field for up to 2 days. In two of three sperm pulses detected, fertilization per day reached 60%. They suggested egg longevity and perhaps slow sperm diffusion re-

sult in fertilization continuing over an extended time period. These findings are relevant to decreased population densities resulting from overfishing. Vavrinc and McNaught reported that populations of *S. droebachiensis* in "no-take" conservation areas along the coast of Maine have not recovered, which indicates the importance of understanding the basis of population biology.

Lytechinus variegatus is widespread on the Florida gulf coast shelf. Cobb and Lawrence found that gonad production in individuals in off-shore populations is much lower than that reported for populations in other locations, suggesting that the off-shore populations are food limited and may have little potential for fisheries.

Sea urchin fisheries will continue to operate, but the questions of size and environmental impact must be addressed. It is essential for the fishery itself to have a thorough understanding of the biology and ecology of the sea urchins involved. Cooperation between the managing agencies and the fisheries will be required.

AQUACULTURE

Most studies included prepared feeds, which are essential for aquaculture. The ability of prepared feeds to support somatic and gonadal production in sea urchins is still of interest. Robinson and Peters showed that individuals fed prepared feeds produced much larger gonads and were >9 times more efficient in gonad production than those fed *Laminaria longicurvis*, *Enteromorpha intestinalis*, or *Ulva lactuca*. Pearce fed kelp or prepared feeds to *S. droebachiensis* ranging from 30 to 70 mm in diameter. Gonad production was greater with the prepared feeds and proportionally greater in small individuals. Gonads from individuals fed prepared feeds were softer than those fed kelp,

undoubtedly reflecting differences in nutrient-reserve cells and gametes.

Interest now is turning towards specific dietary requirements. Wallace et al. found that protein affects gametogenesis differently in males and females and that >23% dry weight protein is the minimal requirement for production and survival. Worrell et al. found that glucose concentration in the coelomic fluid of *L. variegatus* is very responsive to feeding. Glucose concentration falls below 20 mg/dl after only 12 hr in individuals without food from 55 mg/dl in individuals fed a diet rich in carbohydrate. This finding indicates that most digestion and absorption occurs quickly and that a continual supply of food is necessary for maximal production.

Kennedy et al. found that small *S. droebachiensis* elongate and desaturate short-chain (18 C) polyunsaturated fatty acids to long chain (20–22 C) n-3 and n-6 fatty acids. The test had higher proportions of 20:4n-6 fatty acids than do gonads and gut. The sea urchins synthesized 20- and 22-C non-methylene-interrupted dienes at concentrations inversely proportional to dietary and tissue concentrations of n-polyunsaturated fatty acids and highly unsaturated fatty acids.

Ammonia production is a recognized problem in aquaculture. Lawrence et al. found an ET₅₀ of about 80 hr for tube-feet activity for *L. variegatus* and *Paracentrotus lividus* and of >96 hr for *Strongylocentrotus franciscanus* and *Arbacia punctulata*. The pH of individual *L. variegatus* and *A. punctulata* in 1-liter culture vessels increased from 8.1 to 8.9 in 24 hr. Aquaculture of sea urchins will require rigorous water quality control.

Polyculture remains of interest. Shpigel et al. used algae (*U. lactuca* and *Gracilaria conferta*) grown in effluents from fish culture and prepared feed as food for *P. lividus*. Protein absorption was similar with both prepared and algal diets, but protein assimilation efficiency was greater with the prepared diet. Gonad pro-

duction was greater as usual with the prepared diet, but color was better with algae. It should be possible to formulate prepared feeds with carotenoids to produce the desired color.

Shpigel et al. also reported that short daylight periods resulted in greater gametogenesis. Moody and Walker are investigating the molecular mechanism sea urchins use for detecting changes in day length. Pomory found that *S. franciscanus* had smaller gonads under a 4:4 hr repeating light/dark cycle for 2 mo than under 6:6 and 12:12 cycles. He suggested this decrease in production resulted from disruption of feeding by the abrupt change in light. This finding has implications for lighting conditions in aquaculture. The distinction between gonad production per se and gametogenesis is clear.

The great variation in growth of small sea urchins in culture was confirmed by Harris and Madigan with *S. droebachiensis*. Occurrence of quickly growing and slowly growing morphs of *S. droebachiensis* (Vadas et al.) opens the possibility of selection of individuals for seed-stock improvement. Rapid growth to a marketable size may be a major way to decrease cost.

Development of a cost-effective feed that promotes body growth of small individuals and of gonads in large individuals will be a key for successful aquaculture of sea urchins. Future work undoubtedly will focus more on the nutritional requirements for both body and gonad growth. Mechanisms of control of gametogenesis that produce the appropriate gonad state must be better understood. The conditions for aquaculture itself require more study. Collaboration between biologists and commercial aquaculturists, probably with governmental support, will be necessary.

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Plenary Abstracts

Echinoderms of the Gulf of Maine: Occurrence and Exploitation.

JOHN H. DEARBORN, *School of Marine Sciences, University of Maine, Orono, ME 04469.*

The Gulf of Maine is the body of water within the huge indentation of the coastline between Cape Sable, Nova Scotia, and Massachusetts. Its southern border is Georges Bank. The echinoderm fauna of the Gulf of Maine, including Georges Bank, in depths from the intertidal to 500 m, includes the following numbers of species: crinoids, 4; asteroids, 37; ophiuroids, 30; echinoids, 7; and holothurians,

17. This fauna is described briefly and compared with the shallow-water echinoderms of the Florida Keys and Bermuda. Two species of echinoderms from the Gulf of Maine are presently exploited. A regular echinoid *Strongylocentrotus droebachiensis* is harvested primarily for its gonads for Asian markets. Muscles of the body wall of the holothurian *Cucumaria frondosa* are harvested for trepang, and skins are used as a protein supplement in animal feeds and as a fertilizer. The history of the commercial harvesting of these two species is discussed briefly, and present and future ecological concerns are explored. Populations of both species are now much reduced in the Gulf of Maine. Difficult management issues remain unresolved.

There is now reasonable agreement among biologists concerning the validity of an ecosystem approach to management, but for a variety of complex reasons we still tend to regulate by individual species. As new marine resources are exploited, it is difficult to create reasonable regulations before the resource is overfished. Except for relationships between green urchins and algae, there are few long-term quantitative data available on interactions between commercially harvested and non commercial species of invertebrates. Finally, for most of the general public, environmental issues involve vertebrates, especially birds and mammals. There is little knowledge of and thus little concern for echinoderms and other invertebrates. These issues are discussed with special reference to the Gulf of Maine.

Echinoderms as Alien Invaders.

PAUL A. TYLER AND CRAIG M. YOUNG, *Southampton Oceanography Center, University of Southampton, SO14 3ZH, U.K.; Harbor Branch Oceanographic Institution, Ft. Pierce, FL 34946.*

Like most animals and many people, echinoderms sometimes find themselves outside their comfort zones. Larval echinoderms disperse far and wide, sometimes settling in places where they can survive to reproduce, but often landing where they will ultimately perish. This is exemplified by deep-sea echinoids and ophiuroids that settle over broad bathymetric zones but ultimately survive within very narrow depth ranges. Shallow-water echinoderms can often tolerate the temperature and pressure conditions of the deep sea and could potentially invade the deep slope within a single generation. At present, larval invasion appears most likely through cold isothermal water columns near the poles. During the Mesozoic and early Cenozoic eras, many echinoderms, notably the cidaroids, probably invaded the deep sea through a warm isothermal water column similar to the modern Mediterranean. The larval processes that permit invasion are often at odds with the adult processes that permit survival. Nevertheless, the echinoderms provide many useful models for investigating the origin of the deep-sea fauna. In this paper, we examine mechanisms by which shallow water echinoderms may have invaded the deep sea of the past and may be continuing to do so today.

Antarctic Sea Stars and Sea Urchins: How They Changed Major 20th Century Paradigms in Marine Biology.

JOHN PEARSE, *Long Marine Laboratory, University of California, Santa Cruz 95064.*

Two abundant, widespread, shallow-water Antarctic echinoderms, the asteroid *Odontaster validus* and echinoid *Sterechinus neumayeri*, have played major roles in reversing several major paradigms in marine biology that were established during the first half of the 20th century.

“Orton’s rule,” formalized by Thorson in 1946, proposed that temperature change regulated seasonal reproduction, with the corollary that where there was little or no temperature change, reproduction would be continuous. Both *O. validus* and *S. neumayeri* were found to have strongly seasonal reproduction in McMurdo Sound, Antarctica, where sea temperatures are always close to -1.8 C. Subsequently, seasonal reproduction was found for many other Antarctic species, and, in the case of *O. validus*, photoperiodism is now known to regulate the timing of gametogenesis.

“Thorson’s rule,” developed by Thorson in the 1930s and 1940s and formalized by Mileikovsky in 1971, proposed that pelagic development predominated in shallow tropical and temperate marine environments but was rare or absent in polar and deep seas. Again, both *O. validus* and *S. neumayeri* were found to have pelagic, planktotrophic larvae, and, subsequently, most other Antarctic species as well (albeit often pelagic lecithotrophs). The gradient proposed by “Thorson’s rule” disappeared.

Finally, physiology during much of the 20th century held the idea that organisms were temperature adapted, and functions such as respiration and development evolved so that rates would be equivalent

in different environments. The extremely slow rates of respiration, development, and growth in *O. validus* and *S. neumayeri*, and most or all other Antarctic species examined, question this idea. Although it has been proposed that these low rates are an adaptation to low food supplies, evidence now supports the idea that they are due to constraints imposed by low temperature itself. Further work is needed to understand these constraints, using these two species of echinoderms as excellent model animals.

Oral Presentation Abstracts

Why Do Small Brittlestars Have Hemoglobin?

ANA BEARDSLEY CHRISTENSEN, *Biology Department, Lamar University, Beaumont, TX 77710.*

A small ophiactid brittlestar, tentatively identified as *Ophiactis rubropoda*, was collected on the rock jetty in Port Aransas, Texas. These brittlestars inhabit clumps of algae, sponges, and rock crevices. The main body of the brittlestar is often located in a hole, with the arms extended out into the water column in a typical feeding posture. The tube feet on the extended arms periodically contract in a synchronous wave. This ophiuroid possesses hemoglobin contained in coelomocytes (RBCs) present in the water vascular system (WVS). The P50 of the hemoglobin, measured in cellulo, is 27.9 ± 4.1 mmHg (at 20 C [pH 8.0]; $n = 10$; mean \pm SD). The percentage of oxygen (measured in an aerated aquarium) in many of the occupied holes was lower than that of the surrounding seawater (21% [air saturated] vs. 5-13% in the holes). The oxygen levels in the crevices are such that the hemoglobin would be able to unload some of its bound oxygen. The tube foot contraction behavior, coupled with the presence of RBCs in the WVS, may be transporting oxygen to parts of the body (e.g., disc) not exposed to water column. This mode of oxygen transport has been demonstrated in the burrowing ophiuroid, *Hemipholis elongata*, a close relative (Beardsley and Colacino, 1998).

Effect of Dietary Lipids on Fatty Acid Composition and Metabolism in Juvenile Green Sea Urchins (*Strongylocentrotus droebachiensis*).

EDDY J. KENNEDY, JOHN D. CASTELL, SHAWN M.C. ROBINSON, G. JAY PARSONS, TAMMY J. BLAIR, AND ENRIQUE GONZALEZ-DURANT, (EJK, JDC, SMCR, TJB) *Department of Fisheries and Oceans, Biological Station, 531 Brandy Cove Rd., St. Andrews, NB, Canada E5B 2L9;* (EJK, GJP) *Marine Institute, Memorial University, St. John's, NF, Canada, A1C 5R3;* (EG-D) *Biology Department, Dalhousie University, Halifax, Nova Scotia, Canada, B3H 4J1.*

Relatively little is known of the nutritional requirements of sea urchins, especially at the juvenile stages. Lipids are important components in the diets of other cultured marine organisms. One of the costly restrictions on feed formulation for marine fish species is the requirement for fish oils to supply the essential n-3 highly unsaturated fatty acid (HUFA). This study investigated the effects of different dietary lipid sources on the fatty acid composition and metabolism of juvenile green sea urchins (*Strongylocentrotus droebachiensis*). All experiments were conducted in the lab. The juvenile sea urchins were held in plastic floating baskets with a flow-through seawater system where they were fed to satiation. Kelp (*Laminaria longicervis*) served as a control diet. Experimental diets contained 5% of: corn oil (high in 18:2n-6), linseed oil (high in 18:3n-3), menhaden oil (high in n-3 HUFAs 20:5n-3 and 22:6n-3), or 1:1 mixtures of corn oil and linseed oil, or corn oil and menhaden oil or linseed oil and menhaden oil. Unlike marine fish, the sea urchins exhibited ample ability for elongation and desaturation of shorter chain (18 carbon) polyunsaturated fatty acids (PUFA) to longer chain (20 and 22 carbon) n-3 and n-6 HUFA. Thus, 18:2n-6 from corn oil in the diet resulted in high levels of 20:4n-6 in the sea urchin and, similarly, 18:3n-3 in the diet resulted in high levels of 20:5n-6. Even when fed kelp or diets with menhaden oil, the sea urchins did not incorporate high levels of 22:6n-3 into their lipids. In addition to the effects of dietary lipid sources on fatty acid composition of the lipids of total soft tissues of sea urchin, there were great differences in fatty acid composition among different tissues and among lipid classes of these tissues. For example, the test (shell), which is in constant contact with the seawater, incorporated very much higher proportions of 20:4n-6 than the gonad or gut tissues. This may reflect an important role of 20:4n-6 in ion transport and osmoregulation. The sea urchins also synthesized a number of 20 and 22 carbon non-methylene-interrupted dienes (NMID), and the concentration of the major NMID was inversely proportional to the dietary and

tissue levels of n-3 PUFA and HUFA. The significance of these and other interesting aspects of fatty acid metabolism in sea urchins will be discussed.

Gonad and Gut Repletion Indices of the Co-Occurring Sea Urchins *Arbacia punctulata* and *Lytechinus variegatus* on the Central Florida Gulf Shelf.

JANESSA COBB AND JOHN M. LAWRENCE, *Department of Biology, University of South Florida, Tampa, FL 33620.*

Changes in the reproductive and feeding patterns of *Arbacia punctulata* and *Lytechinus variegatus* were monitored at four sites on the central Florida gulf shelf. Both species were found in relatively equal numbers at one offshore and one inshore site. Two additional offshore sites dominated by either *Arbacia* or *Lytechinus* were also sampled. Productivity of each site was estimated by sampling erect fleshy algae to determine total biomass. Gonad indices (GI = $100 \times$ gonad/total body wet weight) and gut repletion indices (RI = $100 \times$ gut contents/total body wet weight) were used to compare changes in feeding and energy allocated to reproduction. Offshore sites were more productive in terms of algal biomass, particularly where *Arbacia* was dominant, and had larger urchins. At the site where *Arbacia* was dominant, individuals had significantly higher RI than at all other sites, which supports the conclusion that this site is more productive.

Although RI did not vary between sites for *Lytechinus*, GI of inshore specimens were significantly higher than at offshore sites. This suggests that the RI is a poor indicator of the amount of food eaten. *Lytechinus* ingests sediment and other inorganic substances that add to the RI value but would not contribute to energy production.

Offshore specimens had consistently higher RI (4.41–13.24) than GI (1.52–7.47) in comparison to the inshore site. Despite greater production at offshore locations, all indices were considerably less than those found in studies from other locations, which suggests that the populations studied here are food limited.

The Effect of Protein on Gonad Development in Small Sea Urchins (*Lytechinus variegatus*).

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Lytechinus variegatus is a viable candidate for commercial aquaculture. Nutritional requirements for this species have not been determined, particularly in juveniles. Juveniles (~14 mm in diameter) were fed ad libitum one of four isocaloric diets varying in protein concentration (12, 19, 27, or 42% of dry weight) for 14 wk. Gonad production occurred in individuals in all diet treatments and at diameters that were smaller than reported in field populations. Individuals fed the 12% protein diet were significantly smaller in diameter and mass and had limited gonad production. Gonad production was similar in individuals fed 19, 27, or 42% protein diet. When image analysis was used, the volume occupied by the gametes and nutritive phagocytes of females and males and long diameters of oocytes were measured from H/E-prepared slides of gonad tissue. The mean oocyte diameter increased directly with protein concentration, and an additional cohort of oocytes was apparently produced at 42% protein. In females, the volume occupied by the germinal epithelium and nutritive phagocytes did not vary among protein levels. In males, the volume occupied by the gametes was significantly reduced in those fed 12 or 19% protein, with a corresponding increase in the volume of nutritive phagocytes. Survivorship was 100% in individuals fed the 27 or 42% protein diet but was reduced to 73 and 57% in those fed the 12 and 19% protein diets, respectively. These data suggest that protein affects gamete production differentially in females and males and that the minimal requirement for protein in *Lytechinus variegatus* is >19%. Funded by a Mississippi-Alabama Sea Grant.

Suspension Feeding in the Ophiuroid *Ophiocoma scolopendrina*: Optimal Foraging or Just a Lot of Arm Waving.

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The ophiuroid *Ophiocoma scolopendrina* exhibits a distinctive pattern of feeding activity on intertidal reef platforms off Kenya. As the first wave of the flooding tide washes over a platform, these ophiuroids engage in a brief (seconds to minutes) burst of suspension feeding, vigorously sweeping the air-water interface and associated sea foam with the ventral surface of two to three arms. Passive suspension-feeding (with arms extended in the water column) is the primary feeding mode throughout the rest of tidal cycle (involving 25–65% of the population at a time); bottom feeding (with arms extended along the substratum) is infrequent (<10%), particularly at high tide (1%). Field experiments show that surface suspension feeding is regulated by water depth and can be triggered by suspended particles. Analysis of particulate food sources indicates a high organic content in sea foam compared with seawater and surface sediments, which suggests that brief bouts of surface suspension feeding contribute disproportionately to the ophiuroid's total energy intake. The degree of exposure of *O. scolopendrina* to predators varies across the tidal cycle. They are least exposed around high tide, when 85–95% of the population is hiding in crevices and holes in the reef. They are most exposed and conspicuous (particularly while surface suspension feeding) at low tide, when predatory fish cannot access the platforms. Suspension feeding behavior in *O. scolopendrina*, therefore, appears to be specially adapted to its intertidal habitat and tidal refuge from fish predation.

Effect of Urchin Size and Diet on Gonad Yield and Quality in the Green Sea Urchin (*Strongylocentrotus droebachiensis*).

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A 6-wk experiment was conducted to determine the effect of urchin size and diet on gonad enhancement of the sea urchin *Strongylocentrotus droebachiensis*. Urchins were divided into four size classes—30–40, 40–50, 50–60, and 60–70 mm test diameter—each being split into two dietary treatments (prepared feed or kelp [*Laminaria* spp.]). Mean yield, color, texture, and firmness of gonads from urchins in each size/dietary treatment combination were determined at 0 and 6 wk, and the relative percentage of change over the 6-wk period was calculated. Gonad taste was subjectively evaluated at the end of the experiment. Percentage of increase in gonad yield over the 6-wk period was greater in urchins fed prepared feed than in urchins given kelp, whereas smaller urchins had a greater percentage of increase in yield than larger individuals. Gonad color improved in almost all treatment combinations and was, generally, better in smaller urchins and in those fed the prepared diet. Gonad texture improved in all treatment combinations except the 60–70 mm size/prepared feed one. Improvement in texture was not significantly dependent on feed type. Gonad firmness decreased in the two smaller size classes and stayed approximately the same in the two larger size classes. Urchins fed the prepared diet produced significantly softer gonads than urchins fed kelp. Kelp-fed individuals produced significantly better-tasting gonads than those fed the prepared diet, although the latter had a taste that was deemed satisfactory to good.

The Efficiency of Prepared Diets for Growing the Green Sea Urchin (*Strongylocentrotus droebachiensis*).

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The continuing development of the sea urchin culture has led to the need for efficient feed for cultured animals. This experiment tested the efficiency of three local seaweeds and one prepared diet to produce gonads in sea urchins as well as how the urchins handled the diets. Sea urchins were collected by divers, randomly divided into eight groups (four treatments × two replicates) of 20 urchins, placed into eight 50-liter tanks in the lab in a randomized block design and supplied with a

continuous flow of seawater. Animals in each tank were provided with one of four diets; *Lamanaria longicirvis*, *Enteromorpha intestinalis*, *Ulva lactuca*, or a prepared pelleted diet. Food was weighed prior to feeding, and any uneaten food was removed and reweighed. At four different periods over the experiment, 12 animals from each tank (24 per treatment) were removed and placed into a bowl that contained filtered ambient seawater for 1 hr. The fecal pellets were then counted and a small sample was weighed. Results showed that the prepared diet produced much higher gonad yields than any of the algae and were more than nine times as efficient at producing gonads per unit of food consumed. Fecal production rates ranged from 10 to 85 pellets per hour. *Ulva* diets were the most variable over time in fecal pellet weight, whereas the prepared diets were the heaviest. The significance of these results to the culture of sea urchins will be discussed.

Sympatric Growth Morphs and Size Bimodality in *Strongylocentrotus droebachiensis*.

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We systematically sampled urchins for two years at two sites (Allen Island [AI] and Schoodic Peninsula [SP]) in the Gulf of Maine. Basic demographic information (density and size structure) was obtained and a subset of urchins aged by counting annual bands on the interambulacral plates. Size-at-age analyses showed that the population at AI consisted of two sympatric growth morphs, fast growing (fg) and slow growing (sg), each described by its own von Bertalanffy growth parameters for mean size and size variance. The two morphs also differed in maximum observed ages (sg 6–11 yr vs. fg 16–18 yr) and in maximum test diameter sizes (sg 30–35 mm vs. fg 50–70 mm). At SP, a single (fg) morph was identified that had growth characteristics similar to the fg morph at AI. A bimodal size-frequency distribution at AI reflects the accumulation of urchins of each morph at asymptotic size.

We advanced several hypotheses, e.g., sex ratios, morphology, genetics, density, spatial distribution, settlement history, and growth history and migration, to explain the origin and coexistence of the two forms. Genetically different larvae or a phased process of differential settlement, migration, and growth seem the most likely cause(s). Interestingly, the sublegal size (<50 mm) and short life span of the sg morph preempts its recruitment into the fishery. Moreover, if the sg morph is widespread and genetically based, intensive harvesting may enhance selection for the sg morph. These findings may have serious implications for understanding the population structure and managing the urchin fishery.

Dimensional Similarity and the Evolution and Growth of Shape in Sea Urchins.

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Skeletons of most regular urchins have characteristic shapes. The shapes of urchins belong to a class of shapes that also describes fluid droplets, submerged attached bubbles, and engineered “echinodomes.” The latter structures are a special type of dome (or tunnel) used for storage of liquids, for underwater domes, or for support of road works over a tunnel. These domes are useful because they minimize the amount of material required in the dome’s wall. Urchins probably do not use this shape to minimize wall material, although the shape may distribute stresses through tensile structures such as sutural ligaments. In urchins, this class of shapes is more interesting in revealing causes of shape during growth. These “developmental” causes of shape can be analyzed to reveal constraints and patterns in the evolution of form. To this end, I present a dimensionless number that characterizes urchin shapes in terms of the relevant forces that uniquely determine their shapes. This dimensionless number compares the product of tension Nm^{-1} in the body wall and the gradient of tube foot forces with depth Nm^{-1} with the square of the internal pressure N^2m^{-1} . The higher the square of pressure relative to the other factors, the rounder the urchin.

Uptake, Accumulation, Bioconversion, and Physiological Functions of Mycosporine-Like Amino Acids (MAAs) in Tropical Holothuroids.

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Most marine organisms contain UV-absorbing, mycosporine-like amino acids that afford protection from solar UV radiation. Like other Metazoa, echinoderms probably cannot synthesize MAAs de novo but instead obtain them from photoautotrophs in their diets. Holothuroids from the Great Barrier Reef contain seven MAAs. Concentrations of MAAs generally are highest in the epidermis and low to undetectable in internal organs, except for ovary, gut, and ectodermally derived tissues, a distribution that initially suggested both their dietary origin and a sunscreensing function.

Several MAAs are present in the sediment and microflora eaten by tropical holothuroids. Bacteria (including *Vibrio harveyi*) in the gut lumen of *Thelenota ananas* stoichiometrically convert the cyanobacterial MAAs shinorine and porphyra-334 to mycosporine-glycine, so that the composition of the digesta changes progressively along the gut. There is a net decline of all MAAs during their passage through the gut, which suggests their translocation to other tissues. There is a concentration-dependent uptake of MAAs across the wall of the isolated gut, from physiological concentrations as low as 10 μ M. The MAA complement in the tissues is more diverse than that of the diet and gut contents, notably in the presence in the former of asterina-330, which may be produced from other MAAs in the holothuroid's tissues. Accumulation from the diet is the major means by which many marine consumers obtain this source of UV photoprotection, and echinoderms are useful test organisms for studying the accumulation, bioconversion, and functions of MAAs, offering the opportunity for integrated ecological, physiological, developmental, and biochemical investigations.

Seasonal Variation in Density and Body Composition of the Commercially Important Sea Cucumber, *Parastichopus parvimensis*.

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The sea cucumber *Parastichopus parvimensis* is currently fished in several areas of the west coast of the United States and Baja California, Mexico, with few restrictions. This is, in part, due to the fact that there is little known about its ecology and reproductive biology. We studied *P. parvimensis* at two sites in Santa Barbara, California, from October 1998 to October 1999. Densities were counted monthly along randomly placed band transects. Throughout the study, trends in sea cucumber densities were similar at both study sites. Densities were low in the fall and began increasing in January, until peak values were reached in June. A steep decline occurred in July, and low densities persisted through October. Body composition was determined each month by collecting and dissecting 30 specimens to assess changes in mass and presence of body parts, including gut, respiratory tree, body wall, and gonad. Body composition varied seasonally. The mean proportion of body wall was highest in the fall, declined January through April, and increased May through October. The mean proportions of dry gonad and dry gut both followed seasonal patterns that were opposite that of the body wall. Evisceration occurred in August, September, October, and December. No evisceration was seen January through July. The results of this study lead to the conclusion that there are distinct and coinciding seasonal trends in reproduction, resource allocation, evisceration, and densities of *P. parvimensis*.

Propagation of the European Sea Urchin (*Paracentrotus lividus*) in an Environmentally Friendly, Land Based Facility.

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The sea urchin *Paracentrotus lividus* was introduced as a candidate species in fish, seaweed, and sea urchin integrated system in Eilat, Israel. Although fish represent the main product, effluents from

fish culture support the growth of macroalgae *Ulva lactuca* and *Gracilaria conferta*. Both seaweeds were used as a biofilter to remove dissolved nutrients from the water and as food for the sea urchins. Sea urchin performances in terms of such as growth, survival, food conversion ratio (FCR), protein and energy use, gonad production, and gonad color were evaluated. Growth rate from spawning to commercial size (45-mm) on seaweed was 30 mo, FCR on a wet weight basis ranged between 5 and 7, and survival rates from settlement were 70–80%. Protein intake was similar for both algal and prepared diets, but protein retention efficiency was greater with prepared diet. Supplementation with a prepared diet enhanced gonad growth, whereas seaweed was necessary for improving gonad color. Diet rotation with the prepared feed followed by *U. lactuca* and *G. conferta* resulted in large, bright yellow-orange gonads. Gametogenesis is negatively correlated with light. Sea urchins exposed to short day-light periods had the greatest reproductive development.

Peristaltic Locomotion and Habitat in Holothuroids.

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Peristaltic locomotion is used by many soft-bodied invertebrates. In previous research, holothuroids were reported to use peristaltic locomotion, although the specific type of peristalsis was not described. In addition, there are few data on differences in locomotion between epifaunal and infaunal holothuroids. The locomotion of four species of holothuroids was studied by use of time-lapse video. *Oncus pygmaeus* (epifaunal) and *Thyonella gemmata* (infaunal) were selected from the Order Dendrochirotida. *Holothuria floridana* (epifaunal) and *Holothuria princeps* (infaunal) were selected from the Order Aspidochirotida. The specific type of peristalsis used by each species was determined from analysis of the time-lapse videorecordings. The results indicate that epifaunal species and infaunal species within a given order use the same type of peristalsis. However, the two orders use different types of peristalsis for locomotion. The two species in the Order Dendrochirotida use direct overlapping peristalsis, and the two species in the Order Aspidochirotida use direct arching peristalsis (Heffernan and Wainwright, 1974. Biol. Bull. 147:95–104).

In addition, stride velocity and crawl velocity were measured from frame by frame analysis of the videotape. Stride velocity is a measure of the time for a peristaltic wave to move the entire length of the animal. Crawl velocity is a measure of the distance the animal travels in a single complete peristaltic wave. The kinematic analysis of peristalsis in the four species shows a general trend of increased stride velocity and crawl velocity with increased body length.

Photoperiod Effects on Gonad Production in the Red Sea Urchin *Strongylocentrotus franciscanus*.

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The red sea urchin is of commercial importance and is harvested for roe. One possible application of aquaculture facilities would be for short-term culture of wild harvested urchins with the aim of increasing gonad size before sale. Therefore, finding conditions that maximize gonad production is of interest. Sea urchins held under a 4:4 hr repeating light:dark cycle for 2 mo had lower amounts of gonad than urchins held under 6:6 and 12:12 hr repeating light:dark cycles. It is suggested that the difference may be due to disruption of feeding.

Patterns of Spawning of the Green Sea Urchin, *Strongylocentrotus droebachiensis*, in Central Maine Over a Three-Year Period.

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A number of proximate factors, such as temperature, phytoplankton blooms, and photoperiod, are thought to control gamete release in echinoderms. Experimental studies have shown how single environmental factors cue spawning; however, long-term field studies are lacking. To determine the

factors that contribute to the variation observed in the timing of green sea urchin spawning, sea urchins and oceanographic variables were sampled biweekly at four sites during the late winter and spring of 1998, 1999, and 2000 in central Maine from R/V *Alice Siegmund* (Island Institute). Analysis of gonad indices showed that spawning was relatively synchronous between sites and sexes and occurred in mid- to late April during each year. During all years, spawning coincided with the first, sustained increase in phytoplankton (chlorophyll *a* concentrations of 1–2 $\mu\text{g/L}$) coupled with a decrease in inorganic nutrient concentrations. Additionally, spawning was significantly correlated with increasing water temperatures (to 5–6 C during the spawning period) in each year. Gonad indices were significantly higher in females than males during the peak of the spawning period, although this difference varied over time and between sites. Interannual variability in spawning was significant: the peak gonad index declined more slowly in 2000 than in either 1998 or 1999. Despite the relatively consistent pattern, there is considerable variability in the timing, duration, and environmental correlates, especially water temperature and chlorophyll *a*, of spawning.

A Molecular Approach to Understanding UV-Induced Mitotic Delay in Sea Urchin Embryos.

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Many studies have demonstrated that ultraviolet radiation (UVR) causes dosage-dependent delays in cell division. Multiple molecular targets of UVR have been investigated in mammalian somatic cells, but they have not been identified conclusively in embryonic cells. Our main objective is to identify molecular targets of UVR that lead to delays in division in echinoderm embryos by investigating signal transduction pathways that affect DNA synthesis and cell division and that are likely to be affected by UVR. As a first step, we defined the UV-sensitive periods in eggs and embryos of the purple sea urchin, *Strongylocentrotus purpuratus*, using controlled UVR wavelengths and dosages. By use of cleavage delay as an endpoint, sea urchin eggs and embryos varied in their sensitivity to UVR during cell division. They exhibited the greatest delay in the first cell cycle when irradiated between 30 and 45 min after fertilization, just after DNA synthesis. Embryos exposed to UVR after 45 min postfertilization (before the first division) experienced no delay in the first division but a significant delay in the next cell cycle. Currently, we are conducting experiments (using specific antibodies and activity assays) to investigate effects of UVR on various signaling pathways, such as the MAP kinase and cyclin-dependent kinase pathways, known to be operating in eggs and early embryos. Preliminary results indicate that UV irradiation of eggs does not affect MAP kinase or DNA synthesis directly but does affect phosphorylation of the cyclin-dependent kinase, *cdc2*, a component of the mitotic promoting factor, which controls entry into mitosis.

Testing the Costs of Small Egg Size in Echinoderms.

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An extensive literature exists concerning the evolution of life history strategies in echinoderms. Much of this literature is based on empirical data, and theoretical models that suggest egg size is an important predictor of developmental mode. Small eggs tend to develop indirectly as feeding larvae with an extended planktonic period, whereas large eggs tend to develop directly, with little or no time spent in the plankton. In echinoderms that develop indirectly from small eggs, embryological experiments have shown that separating blastomeres at the two-cell stage can yield two completely viable offspring that will grow and develop normally (although at a smaller size). This observation has led many researchers to ask the question, why don't echinoderms produce the smallest eggs capable of development? In a series of laboratory experiments I addressed one of the potential costs of developing from small eggs: do embryos and larvae developing from small eggs suffer increased rates of predation? Blastomeres of the Pacific sand dollar *Dendraster excentricus* were separated at the two-cell stage and reared to produce halved and full-size larvae. Sibling halved and full-size larvae were presented as prey items to several common planktonic predators: (1) crab zoea, (2) crab megalopae, (3) chaetognaths, and (4) postlarval fish. Larvae were presented as prey items at several developmental stages from prism larvae through eight-arm plutei. Crab zoea and chaetognath predators consumed significantly greater numbers of halved larvae than full-size larvae. Postlarval fish showed the opposite

trend, consuming significantly more full-size larvae than halved larvae. Crab megalopae showed no preference in the numbers of prey items consumed. For all of the treatments, differences in predation rate were greatest at early developmental stages, when size differences between full and halved larvae were also greatest. These results suggest that the direction of selection on egg size, as a result of planktonic predation, will vary with the presence and abundance of particular predators.

Thyroxine Induces Facultative Feeding in an Obligatorily Feeding Sand Dollar Larva.

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Lecithotrophic development has evolved from planktotrophic development numerous times in many marine invertebrates and echinoderms. The evolutionary transition from planktotrophy to lecithotrophy involves changes in developmental timing and patterning and is generally considered to be irreversible. Lecithotrophic larvae develop from relatively large yolky eggs that provide the organism with sufficient energy to develop to metamorphosis without exogenous food. Some echinoid and gastropod larvae have the capacity to feed facultatively (facultative planktotrophy). These larvae can develop to metamorphosis without food although functional feeding structures are present. Facultative planktotrophy presumably represents an intermediate developmental mode between planktotrophy and lecithotrophy. Herein we test the hypothesis that an obligate feeding larva with a relatively large egg can develop to metamorphosis without food when larval development is experimentally accelerated with thyroxine. Larvae of *Leodia sexiesperforata* developed to metamorphosis without exogenous food when treated with thyroxine, whereas the starved controls did not reach metamorphosis over the duration of the experiment. By definition, these thyroxine-treated larvae can therefore be considered facultative planktotrophs. Juveniles from the experimental treatment were significantly smaller than juveniles developing with exogenous food; however, adult features such as spines and skeletons appeared normal. On the basis of the present data, we hypothesize that thyroxine plays a major role in echinoderm metamorphosis and the evolution of life history transitions in this group. Moreover, we suggest that juvenile size might have a much stronger influence on adult fitness in echinoids than has been previously recognized.

Spawning and Development of the Sea Star *Pilaster charcoti* During the Springtime Depletion of Ozone in Antarctica.

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Seasonal declines in stratospheric ozone over Antarctica increase the intensity of biologically harmful UV-B radiation entering surface waters. The common astropectinid sea star *Pilaster charcoti* spawns during October and early November, when significant ozone losses occur. The spawn consists of large, yolky eggs that are positively buoyant both in vitro and in situ. On the basis of in situ flotation rates of 0.43 ± 0.13 cm/sec, embryos could reach the surface from a spawning depth of 30 m within 18 hr, before the first four blastomere divisions are completed. Subsequent development through a convoluted blastula, a barrel-shaped larva, and a bilobed larva is similar to that of other astropectinids, but metamorphosis takes place >2 mo after fertilization. Experimental exposure of eggs and embryos from individual females to ambient UV radiation in outdoor tanks showed a significant but moderate relationship between development success and UV-B dose ($R^2 = 0.32$, $P < 0.001$). Other factors, including large differences in the volume and the protein, lipid, and carotenoid weight of eggs from different females might influence this relationship. Despite these individual differences, experiments carried out in situ revealed that high UV-B intensities during clear days with a depleted ozone column caused significant embryonic damage to a depth of 5 m below the surface ($R^2 = 0.81$, $P < 0.001$). *P. charcoti* and other species with positively buoyant eggs may be especially vulnerable to the higher levels of UV-B radiation brought about by ozone depletion over Antarctica.

Fertilization Dynamics in a Temperate Sea Urchin, *Strongylocentrotus droebachiensis*.

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Previous short-term experimental studies have suggested that successful fertilization in many free-spawning echinoderms may be limited by rapid gamete dilution after spawning. However, reproductive traits such as the release of gametes in viscous fluids and extended egg longevity may facilitate fertilization during natural spawning events. To determine the importance of such adaptations, we carried out a series of flume, laboratory, and field studies with the northern temperate sea urchin *Strongylocentrotus droebachiensis*. In a flow-through flume at two different velocities (~2.5 and ~8.5 cm/s), we found that gametes can take several hours to disperse from the test and that >80% of eggs are fertilized in a relatively fixed location, either on the aboral surface of the female or in the eddy immediately downstream of the female. In a laboratory experiment, we found that up to 75% eggs are fertilizable for 72 hr (even up to 96 hr in some cases) in aged but otherwise untreated sea water. In a field study, we suspended sperm-permeable baskets of eggs in the field and sampled them with replacement every 24–48 hr. We detected three sperm pulses during the 1999 spawning season, and per day fertilization levels reached a maximum of 60%. We also used the distribution of cleavage stages at the end of each sample interval to back-calculate the time of fertilization. In two out of the three events, egg longevity, aided perhaps by slow sperm diffusion rates due to “sperm stickiness,” increased total fertilization levels by permitting fertilizations to accrue over an extended time period.

Inductive Signals in Rudiment Development in the Direct-Developing Sea Urchin *Heliocidaris erythrogramma*.

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The echinoderm juvenile develops within the larval body, with its own set of radially symmetric adult axes entirely separate from the larva's bilateral ones. Clearly, echinoderm ontogeny has undergone major evolutionary changes since the bilaterally symmetric ancestor. But little is known about the mechanisms that control juvenile development. We studied juvenile rudiment formation in the direct-developing sea urchin *Heliocidaris erythrogramma*, taking advantage of its large eggs and fast development. The rudiment forms as in indirect-developing sea urchins, by an interaction between the vestibular ectoderm and the left coelom (which arises from the archenteron), giving rise to the pentamerous water vascular system, podia, and nervous system. We investigated inductive signaling between these two layers microsurgically. After early archenteron removal, gastrula ectoderm developed normal larval structures, including vestibule, but no juvenile structures. Archenteron that was removed and then reinserted developed into gut and coeloms and rescued rudiment development. In the presence of gut and left coelom together, juvenile structures developed, but in the presence of gut alone, they did not. Therefore vestibule development is autonomous to the ectoderm, but subsequent rudiment development requires signals from the left coelom. This is confirmed by gene expression patterns. Normally, ectodermal *HeET-1* expression ceases in the newly formed vestibule. In the absence of coelom, it regulates normally, reflecting autonomous vestibule development. *HeARS* expression normally ceases in the vestibule floor (apposed to left coelom) but persists in the vestibule roof. In the absence of coelom, it persists throughout the vestibule, which indicates a downstream response to coelomic signaling.

Morphological Plasticity in Echinoplutei with Different Degrees of Maternal Investment.

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Animals face a heterogeneous environment with respect to food. When feeding in an unpredictable environment, some animals are able to modify ingestive and digestive morphology and/or physiology in order to increase nutrient acquisition. Previous research has shown planktotrophic (i.e., feeding) echinoid larvae respond to the concentration of food in the environment by altering their phenotype to increase ingestion rates. In food-scarce environments, the larvae elongate their arms, to increase

water clearance rates and therefore amount of food captured. What has not been addressed in echinoid larvae is morphological plasticity with different degrees of maternal investment (i.e., egg size). A larger maternal investment results in a reduction in energy required from exogenous food to complete development. A decreased dependence on food may alter digestive strategies. We tested for plasticity of larval arm length and stomach area in three Florida echinoid species with different egg sizes (*Mellita quinquesperforata*, 110 μm egg diameter; *Clypeaster subdepressus*, 150 μm ; and *Leodia sexiesperforata*, 210 μm) in three food environments (2, 6, and 8 algal cells μm /liter). Measurements of postlarval arm length and stomach cross-sectional area indicate that the expression of plasticity is dependent on maternal investment. *Mellita* and *Clypeaster* larvae both expressed plasticity of larval arms and stomach 3 d postfertilization. *Leodia* larvae did not show any change in larval morphology over time in the different food treatments. These results suggest that there are costs to phenotypic plasticity that larvae with a large amount of endogenous energy do not pay.

Population Differences in Reproductive Output and Larval Development for the Sand Dollar *Mellita isometra*.

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The present study investigates variation in population structure of the sand dollar *Mellita isometra* in two barrier islands along the coast of Georgia and the effects of diet and salinity on larval development. Data from the last 2 yr indicate that sand dollars tend to be bigger at Wassaw Island (8–10 cm in diameter) and smaller at Tybee Island (5–6.5 cm in diameter). The adult sand dollars have a spawning season from April until October, and the size of the eggs produced are between 130 and 150 μm . Egg size and numbers varied significantly between large and small females at a site and between sites. The eggs were slightly larger at Tybee Island compared with Wassaw Island, and smaller females spawned more eggs than bigger females. Larval growth and development were directly affected by salinity and diet: larvae grew and developed faster when given mixed algal diets composed of combinations with *Isochrysis* than when fed single algal diets of *Dunaliella tertiolecta*, *Chaetoceros muelleri*, or *Isochrysis galbana*. Lower salinities did not affect growth rates of the larvae, but the onset of the rudiment was delayed. Salinity and diet do not appear to have any effect on survival rates of the larvae.

Juvenile Growth in the Green Sea Urchin: Addressing a Major Bottleneck to Successful Aquaculture.

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Juvenile growth variation in the green sea urchin, *Stongylocentrotus droebachiensis*, represents an important bottleneck to urchin aquaculture in the Gulf of Maine. Repeated growth studies with field-collected and laboratory-reared juvenile urchins show similar patterns of variation in growth rate within cohorts. Newly settled urchins raised from parents selected for fast growth from animals cultured from juveniles since 1998 showed the same pattern of a wide range of growth rates. The offspring of laboratory-cultured parents appeared better adapted to laboratory conditions than those obtained from field-collected parents. The use of suspended caging systems shows promise as cost-effective method for juveniles grow out and has demonstrated a surprising ability of small urchins to respond to favorable conditions within a few days.

Molecular Phylogenetic Evidence Suggests That the Ancestral Echinoderm May Have Closely Resembled a Mobile, Worm-Like Enteropneust with Filter Feeding Gill Slits.

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The deuterostome phyla include Echinodermata, Hemichordata, and Chordata. Careful analyses of a new 18S rDNA data set indicates that deuterostomes are composed of two major clades: chordates and echinoderms hemichordates. Hemichordates include two distinct classes, the enteropneust worms and the colonial pterobranchs. Most previous hypotheses of echinoderm origins have suggested that

the morphology of the ancestral echinoderm looked like a pterobranch that fed using ciliated tentacles. I present a molecular phylogenetic analysis of deuterostomes, with emphasis on resolving echinoderm ancestry, that challenges this longheld view. These data show that pterobranchs may be derived within enteropneust worms, rather than being a sister clade to the enteropneusts. The nesting of the pterobranchs within the enteropneusts dramatically alters our view of the evolution of the echinoderm body plan and suggests that the ancestor to the echinoderms may have more closely resembled a mobile, wormlike enteropneust than a sessile, tentaculated pterobranch. An investigation of the feeding behavior of the acorn worm *Harrimania planktophilus* suggests a novel form of enteropneust feeding that has significant phylogenetic implications. *H. planktophilus* is a facultative filter feeder that has pharyngeal gill slits, similar to fossil cornutes. This study suggests that (1) the gill slits of fossil echinoderms may also have had a filter feeding function and (2) filter feeding gill slits are not an innovation of the chordates but evolved prior to the evolutionary divergence of the hemichordates + echinoderms and the chordates.

Preliminary Phylogeny of Seven Morphological Variants of *Echinaster* (*Othilia*) from the Gulf of Mexico and Caribbean.

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The Echinasteridae (Asteroidea: Spinulosida) are represented in the Western Atlantic by two genera, *Henricia* and *Echinaster*. On the basis of the presence of well-developed crystal bodies, absence of actinal plates, and a regular primary skeleton, *Echinaster* has been divided into two subgenera *E. (Echinaster)* and *E. (Othilia)*. In terms of their biodiversity and systematic relationships, the *Echinaster* complex has been referred to as one of the most enigmatic groups of asteroids in the Western Atlantic. A review of the pertinent literature suggests that this complexity may be due to these sea stars diversifying into local forms. The most recent taxonomic revision of *Echinaster* from the Western Atlantic used 18 morphological characters to delineate five species of *E. (Othilia)* and numerous variants from the Gulf of Mexico and Caribbean. Using the characters from previous studies along with an additional 67 morphological characters, we examined seven color morphs from five populations from the shallow waters (<30 m) off the western Florida coast. Phylogenetic analyses resulted in 692 most parsimonious trees with a length of 534 steps. The genus *Echinaster* was recovered as nonmonophyletic, with the placement of *E. (Echinaster) sepositus* as sister to *Henricia*. The *E. (Othilia)* was recovered as a monophyletic group supported by five apomorphic characters. Further analysis recovered four monophyletic groups: *E. (O.) sentus* and three currently undescribed forms. Two described species, (*E. [O.] spinulosus* and *E. [O.] paucispinus*) were recovered as paraphyletic. This analysis suggests new insights into the biodiversity of the *E. (Othilia)* from the Gulf of Mexico and the relationships between the *Echinaster* subgenera and *Henricia*.

Taxonomy and Evolution of the Family Scutellidae (Echinoidea: Clypeasteroidea) During the Oligo-Miocene.

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The family Scutellidae includes five genera: *Scutella*, *Parascutella*, *Parmulechinus*, *Samlandaster*, and possibly *Scutulium*. Until recently, most of the species were placed into the genus *Scutella*, although the definition of this genus was revised by Durham (1953), thus restricting its usage to a single species. Unfortunately, Durham's work was largely ignored by subsequent authors working with scutellids. Because the name *Scutella* was initially used for many, if not most, scutelline clypeasteroids, there are ~150 nominal species of *Scutella*, including both Old and New World forms.

A thorough revision of the family Scutellidae is under way. First results show that ~60 nominal species, including all non-European forms, can be excluded from the family. Furthermore, only very few species can be assigned to the genus *Scutella* (sensu Durham, 1953). Most of the species belong to the genus *Parascutella* and a second, new, genus. Moreover, many species turned out to be junior synonyms of other species, in particular many paratethyal scutellids are synonyms of Mediterranean species.

The first scutellids appear in the Middle to Late Eocene, with *Samlandaster*, followed by *Parmulechinus*

in the early Oligocene, and *Scutella* and *Parascutella* in the late Oligocene. The group reaches its acme in the Lower to Middle Miocene (Burdigalian-Serravalian), both in species richness as well as in spatial distribution (from Portugal in the west to Iran in the east). The family Scutellidae disappears in the Upper Miocene, the last species occur in the Tortonian of France. Throughout the Oligo-Miocene, a macroevolutionary trend of phyletic size-increase (Cope's rule) can be observed within this lineage.

The family Scutellidae seems to be a relatively basal branch within the Scutellina, retaining continuous interambulacra, having only slightly enlarged interambulacral basicoronal plates, and having interambulacra, which are nearly as wide as the ambulacra at the ambitus. Durham, J. W. (1953): Type Species of *Scutella*. *J. Paleont.* 27/3:347-352.

Phylogenetic Analysis of the Goniasteridae (Asteroidea): *Calliaster* and Kin-A First Step.

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Preliminary phylogenetic analysis of the Goniasteridae has discovered that four genera, *Calliaster*, *Mabahissaster*, *Mitteliphaster*, and *Astrothavma*, are well-supported as a monophyletic clade. Additional material of these poorly known taxa from new collections made over the last 50 years from several institutions has provided the basis for a reevaluation of the ontogeny, systematics, biodiversity, and phylogenetic relationships of these taxa. A cladistic analysis of 46 skeletal characters was performed for the 19 species within these genera to test monophyly of the genera within the clade.

The analysis returned two most parsimonious trees with 175 steps. *Calliaster baccatus* is reconstructed as the sister group to a clade containing the other species from *Calliaster*, *Mabahissaster*, *Mitteliphaster*, and *Astrothavma*. There are three major diversification events within the two major lineages in the crown group. The phylogenetic hypothesis shows that the current concepts for *Calliaster* and *Mitteliphaster* are paraphyletic. Although Bremer and bootstrap support for these tree topologies is low, our knowledge regarding homologies and morphological variation in these species is still relatively poor.

Phylogenetic hypotheses suggest some broad biogeographic patterns, including a dichotomy between species from the Central-South Pacific Ocean and Indian Ocean regions. *C. baccatus*, the sister group to the main *Calliaster* clade, occurs only in South Africa. Phylogenetic data presented here do not support Briggs' (1999) 'Center of Origination' biogeographic hypothesis and are more consistent with patterns seen in *Acanthaster planci* and other marine invertebrates.

The Small, the Large, and the Weird: Phylogenetics of the Laganine Sand Dollars.

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Recent classifications of the Clypeasteroidea (sand dollars and allies) recognize three distinct clades (Clypeasterina, Laganina, and Scutellina). The extremely diverse Laganina arguably contains the strangest of all the clypeasteroids. Although many of the presently recognized genera are of medium size (~50 mm test length), the Laganina contains the smallest of all the sea urchins (<10 mm test length), as well as some large forms (>90 mm test length).

Phylogenetic analyses focusing on fossil and extant forms have indicated that a monophyletic Laganina also includes the bizarre rotulids. *Fibulariella*, a subset of miniaturized laganines formerly regarded as part of the family Fibulariidae, is demonstrably more closely related to rotulids than to fibulariids. Therefore, within the Laganina there were at least two separate derivations of very tiny, almost spherical clypeasteroids lacking peripheral, internal buttresses and pillars.

Species-level analysis of a clade of "true" fibulariids, *Fibularia*, reveals at least two undescribed species. A phylogeny of *Fibularia* shows that the crownward forms are even more reduced and globose than basal ones. Most importantly, separation of *Fibulariella* from *Fibularia* makes much greater sense of the biogeographic and paleontological data for these two very different (but unfortunately similarly named) genera.

Peronella and *Laganum*, two of the most diverse and commonly encountered extant, medium-sized genera, are not monophyletic. Some features used in the past to diagnose these two genera are not phylogenetically informative for these groups. Fossils from North America and Europe can also be placed in this phylogeny, yielding divergence times for some clades.

What Can the Evolution of Development Tell Us About Echinoderm Origins?

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The members of the phylum Echinodermata are some of the most recognizable and well-studied marine invertebrates. Many aspects of echinoderm biology, including their embryology, ecology, and fossil record, have been studied extensively. However, there is little consensus among neontologists or paleontologists about how the group originated. This lack of agreement is not due to a lack of proposed theories. On the contrary, the origin of unique echinoderm features presents such a perplexing mystery to biologists that there are almost as many ideas about echinoderm origins as there are echinoderm biologists. Most of these theories focus on the explanation of a few key features of echinoderms, such as the pentaradial symmetry of the adult, the left-right asymmetry in the larva, or the water vascular system. Despite the availability of extensive embryological, anatomical, fossil, and molecular data, there have been few systematic comparisons of alternative views. Herein, we review the most prominent proposed scenarios for echinoderm origins and discuss some testable predictions about echinoderm biology that can be made on the basis of these scenarios. This explicit discussion of predictions reveals some notable similarities and differences between proposed theories. Most of the theories of echinoderm origins discussed here make unique predictions about the relationship of echinoderm body axes to the anterior-posterior axis of other bilaterians. These predictions may be testable on the basis of developmental data, including the expression patterns of developmental genes. It has been suggested that the expression pattern of Hox genes, which are expressed linearly along the anterior-posterior axis in many metazoan groups, will indicate the echinoderm homologue of this axis. However, the Hox expression data currently available are not entirely consistent with any of the predictions about the anterior-posterior axis of echinoderms that are implied by proposed models. We therefore suggest that additional developmental data should be used to further evaluate these predictions.

Genetic Diversity in the Brooding Sea Cucumber *Synaptula hydriformis* Using Randomly Amplified Polymorphic DNA (RAPD) Analysis: Implication for Method of Fertilization.

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The viviparous sea cucumber *Synaptula hydriformis* is a simultaneous hermaphrodite that maintains multiple broods within the perivisceral coelom. It is an epiphytic species that clings to drift macroalgae, fleshy and calcareous attached algae, blades of seagrass, and the submerged roots of mangrove trees. Over the last century, there has been much disagreement over the method of fertilization. Authors of recent studies suggest that this species is a facultative, if not obligate, self-fertilizer. *Synaptula hydriformis* presents an intriguing case study for genetic diversity, because its life history could involve relatively little gene flow among geographically isolated populations, even with complete out-crossing. Randomly amplified polymorphic DNA (RAPD) analysis is being used to assess rates of self-fertilization and cross-fertilization in *S. hydriformis* collected in central and southern Florida. RAPD banding patterns of the brooded young will be compared with those of the maternal adult. RAPD analysis will also be used to examine the genetic diversity at several geographic scales: brood, algal clump, collection site, and within the Western Atlantic. Currently, RAPD primers are being screened and chosen on the basis of their reproducibility, ability to be easily scored, and the number of polymorphisms produced. This research is funded in part by the PADI Foundation.

Advancing History: Phylogenetics of Tooth Promotion in Echinoid Lanterns.

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Echinoid teeth grow constantly, to compensate for wear at their occlusal ends, each tooth moving forward along the tooth slide of the supporting pyramid of the lantern. The tooth is advanced by the recently discovered dental promotor muscle, which originates on the styloid process of the pyramid and inserts on the sheath of connective tissue surrounding the tooth. The presence of styloid processes

can be taken as evidence for the existence of dental promotor muscles, much as the lantern supports around the peristome indicate the presence of lantern retractors and protractors.

To explore the phylogenetic history of the styloid processes, we have examined representatives of all major post-Paleozoic clades, including irregular echinoids that have lanterns. By mapping symphyseal views of their demipyramids onto currently accepted phylogenies, we can document post-Paleozoic evolution of the styloid processes. Although they are always present, they are expressed to varying degrees and are positioned slightly differently among the major clades.

Styloid processes can be detected in Paleozoic forms as well. From the literature, we were able to identify styloid processes in a palaechinid, three lepidocentrids, a hyattechinid, and an archaeocidarid. Examination of pulls of *Echinocystites pomum* also revealed the presence of styloid processes, and therefore dental promotor muscles, in echinoids as early as the Silurian. However, styloid processes remain undetected in the most basal members of the echinoid clade (e.g., *Aptilechinus*, *Ectinechinus*, or *Aulechinus*). We are also unable to say whether ophiocystioids, which have lanterns remarkably like those of the echinoids, had dental promotors.

Mirror-Image Abnormalities (Situs Inversus Viscerum) in Echinoderms.

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In the echinoderms, situs inversus viscerum (SIV) has been reported in edrioasteroids, crinoids, asteroids, and echinoids. SIV echinoids may comprise <0.1% of a population; they can be recognized externally because the anus is placed anteriorly rather than posteriorly in the periproct, and internally, the last loop of the intestine runs counterclockwise rather than clockwise. The reversal is profound, for even the crystal axes in the SIV apical system are reversed (Raup and Swan, 1967). In normal echinoids, the young echinoid develops on the left side of the larva. Marcus (1981) proved that SIV echinoids are derived from larvae in which the young echinoid develops on the right side of the larva rather than the left. Where do SIV larvae come from, and how is SIV transmitted to offspring? SIV adult *Lytechinus variegatus* were collected in Bermuda in 1974 and Florida in 1993 and 2001 and induced to spawn. Larvae were reared from the following: SIV eggs \times normal sperm, SIV sperm \times normal eggs, and normal sperm \times normal eggs (as controls). All larvae derived from SIV eggs \times normal sperm were SIV. All larvae derived from SIV sperms \times normal eggs were normal. In echinoids, therefore, maternal effects, where the phenotype of the offspring is dictated by mitochondrial DNA in the cytoplasm of the egg, are pervasive, and the SIV is transmitted by the female. In related research, preliminary morphological studies of presumed hybrids between *Encope michelini* and *Mellita isometra* from eastern Florida lead to the hypothesis that the hybrids were derived from *Mellita* eggs fertilized by *Encope* sperms. This has yet to be tested.

Adhesive Proteins from the Cuvierian Tubules of the Holothuroid *Holothuria forskali*.

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When irritated, individuals of the sea cucumber *Holothuria forskali* expel a few Cuvierian tubules, which considerably lengthen, become sticky upon contact to any object, and rapidly entangle and immobilize most potential predators. In this study, we have investigated the cellular origin and composition of the Cuvierian tubule adhesive. Glue prints, which consist of patches of adhesive material left on the substratum after mechanical detachment of the tubule, have been used as a starting material because they are considerably enriched in adhesive secretions. Polyclonal antibodies have been raised against glue print material and were used to locate the origin of glue print constituents in the tubules. Extensive immunoreactivity was detected in the secretory granules of mesothelial granular cells, which suggests that their secretions make up the bulk of the adhesive material. Weak immunolabeling in the other tissues indicates, however, that glue print material may occasionally incorporate other constituents such as, for example, collagen. Glue print material is composed of 60% proteins and 40% carbohydrates. Although it is highly insoluble, a small fraction of this material can be solubilized by use of denaturing buffers. Electrophoretic analysis of the extract revealed that it contains ~10 proteins with apparent molecular weights ranging from 20 to 220 kDa and with similar amino acid composi-

tions. One of these proteins, a 45-kDa protein, is also a prominent protein in whole tubule extracts, from which it has been purified and partially characterized. Partial amino acid sequences from this protein bear no similarity to any known protein. It appears, therefore, that although the adhesive from the Cuvierian tubules of *H. forskali*, like those of most other marine bioadhesives, is protein-based, its composition differs from that of the adhesive secretions of marine invertebrates described so far.

Population Biology of the Fissiparous Brittlestar *Ophiocomella ophiactoides* (H. L. Clark) in Sponge and Algal Habitats.

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The fissiparous brittlestar *Ophiocomella ophiactoides*, previously reported from algal habitat, is reported here for the first time living in association with sponges from Lake Surprise, Key Largo, Florida. The distribution of *Rhizophora mangle*, mangrove sponges, and sponge-dwelling populations of *O. ophiactoides* within Lake Surprise was surveyed along 8.5 km of shoreline. Size-frequency distribution, regeneration category, density, and sex ratio were determined for both sponge- and algal-dwelling populations of *O. ophiactoides*. Results indicate that the presence of *O. ophiactoides* is dependent on sponge diversity and abundance. Collection sites with high sponge diversity and abundance had a higher proportion of *O. ophiactoides* present. Nine sponge species or morphotypes were found, all of which contained *O. ophiactoides*. These include *Chondrilla nucula*, *Clathrina coriacea*, *Halichondria magniconulosa*, *H. melanadocia*, *Haliclona hogarthi*, *Ircinia strobilina*, *Lissodendoryx isodictyalis*, and *Tedania ignis*. Both sponge- and algal-dwelling populations of *O. ophiactoides* had skewed distributions and were dominated by individuals with a small body size and recent signs of fission. Populations in both habitats had densities >100 individuals/dl. About 90% of *O. ophiactoides* observed were unsexable, with no visible gonads present. Males statistically dominated the populations in both habitats.

The Effect of Salinity on Respiration, Excretion, Regeneration, and Production in the Brittlestar *Ophiophragmus filograneus*.

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Ophiophragmus filograneus is a unique echinoderm, because it occurs in estuaries at reduced salinities and not in the open sea. The question is whether this distribution is because it is adapted to reduced salinities or whether some other factor is responsible. If it is adapted, it should function better at reduced salinities. To ascertain whether this is true, *O. filograneus* were collected from Tampa Bay at a salinity of 22‰ and respiration, excretion, regeneration, and production were measured at 16, 22, and 30‰ salinity. Individuals in 16‰ S respired at a lower rate, excreted at a higher rate, and regenerated less than those in 22‰ or 30‰ S. Production (increase in organic material) occurred in the discs and arms and oral frames of individuals in 22‰ and 30‰, but not in 16‰ S. *Ophiophragmus filograneus* was stressed in 16‰ S, because production was less than in 22‰ and 30‰ S. Because *O. filograneus* functions better at high salinities, its restriction to estuaries is probably due to other factors such as food resources, sediment type, competition, and/or predation.

Effects of Variable Water Motion on Regeneration of *Hemipholis elongata* (Say, 1825) (Echinodermata: Ophiuroidea).

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Echinoderms display phenotypic plasticity in material allocation during regeneration. Measurement of variable rates and patterns of arm regeneration under different environmental stresses or toxic conditions may provide a means to assess sublethal effects of ecosystem modification. To determine whether increased water motion affects patterns of regeneration, individuals of the subtidal burrowing brittlestar *Hemipholis elongata* were subjected to laboratory-controlled turbulence conditions. Replicate

aquaria were constructed in which the treatment half of the tank experienced primarily oscillatory (wavelike) turbulence while the control half had no turbulence. Individual brittlestars from which arm tips had been removed were allowed to burrow in randomly placed 6.5 cm diameter cores and allowed to regenerate for a period of 40 d at 20 C, when regeneration was between 39 and 71% complete. Regenerated arm-tip length, weight (dry, skeletal, and tissue), and overall vertebral ossicle size were measured and tested for significant differences between organisms in calm and turbulent conditions. An analysis of variance indicated a significant difference in the regenerated arm-tip length between control and treatment, but not in regenerated arm-tip dry weight or skeleton/tissue ratio of regenerated arm tips. To quantify plasticity in the skeleton, 15 morphological measurements, characterizing overall ossicle size, were made on the proximal faces of 10 vertebral ossicles/individual by use of scanning electron microscopy and image analysis software. Multivariate analysis of variance found a significant difference in the overall size of the vertebral ossicles between treatments, but a discriminant analysis could not determine which of the measurements contributed most to the difference. The results of this study indicate that regeneration in *H. elongata* is a highly controlled process that can be modified by environmental conditions.

On the Relationship between the Parasitic Ciliate *Orchitophrya stellarum* and its Asteriid Hosts.

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Orchitophrya stellarum parasitises asteriid sea stars in the North Atlantic and Pacific oceans. The ciliate has been found in smears and histological sections of testes and in the spawn and external surface of male and female *Evasterias troschelii*, *Leptasterias* spp., and *Pisaster ochraceus* from Puget sound, Washington, and from the spawn of *Asterias forbesi* and *Asterias rubens* from the Isle of Shoals, New Hampshire. *O. stellarum* grows in 5–30‰ S seawater supplemented with 0.01% yeast extract at 8 C. The duration of the posterior contractile vacuole cycle increases with ambient salinity. Uninfected male *L.* spp. were experimentally infected with seawater cultured *O. stellarum*. Effects of *O. stellarum* on sea stars were inferred from statistically fewer males than females for 6 of 10 collections of *P. ochraceus* and 1 of 4 collections of *E. troschelii*; however, no collections of *L.* spp. or *A. forbesii* and *A. rubens* exhibited sex ratios that deviated from 1 : 1. Males were smaller than females in one of two collections of *E. troschelii* and in three of four collections of *P. ochraceus* in 1999; there were no gender-related size differences in the collections in 2000 and 2001. No collection of *L.* spp. exhibited gender-related differences in size. Only two of nine collections of *L.* spp. exhibited a reduction in the testes indexes of parasitized, compared with unparasitized males collected simultaneously; no differences were observed in the parasitized and unparasitized testes indexes of larger *A. forbesii*, *A. rubens*, *E. troschelii*, or *P. ochraceus*.

New Records of Echinoderms from the Gulf of Mexico.

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Two echinoids and one seastar, collected or photographed in the Gulf of Mexico since 1985, constitute new distributional records. *Calocidaris micans*, formerly reported from Cuba, Yucatan Channel, and Barbados, was photographed and collected in the northeastern Gulf of Mexico off Alabama/Mississippi at 100 m. Unpublished museum holdings (USNM) add a second record off Louisiana at 129–144 m. *Pseudoboletia maculata* is an Indo-West Pacific echinoid recorded also in the Atlantic basin at Ascension and St. Helena islands, Venezuela, Barbados, and off Miami, Florida. An unpublished document records this echinoid from the western Gulf of Mexico. Our collections and photographs from off Pensacola, Florida, at ~40 m depth reveal that *P. maculata* occurs there in mixed-species aggregations with the echinoid *Lytechinus variegatus*. *Mithrodia clavigera*, an asteroid from the Indo-West and eastern tropical Pacific and from Brazil, was recently reported from Yucatan Channel and Nicaragua. Several specimens are visible in a photograph taken at ~60 m on 28-Fathom Bank in the western Gulf of Mexico. We also have *M. clavigera* from the Atlantic Ocean off West Palm Beach (32 m) and Fort Lauderdale (<6 m), Florida. Although these records probably are not range extensions within recorded human history, they might represent (re)invasion of the Gulf of Mexico within the last 10,000

yr as appropriate patchy biotope at intermediate depths became available with sea-level rise, with declining influence of the cold low-salinity meltwater of the Laurentide Ice Sheet in the Gulf of Mexico and adjacent waters, and with reestablishment of the Gulf Stream.

Thyroid Hormones, Phenotypic Plasticity and Life History Evolution in Three Classes of Echinoderms.

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Thyroid hormone (specifically T3 and T4 [thyroxine]) effects on growth and metamorphosis in amphibians have been well characterized. Recently, analogous effects of thyroid hormone on echinoderm (asteroid and echinoid) larval development have been described. Intriguingly, the planktonic algae that these larvae feed upon synthesize substantial levels of both T3 and T4 (thyroxine). Thyroxine effects on echinoderm larvae include acceleration of development to metamorphosis, and, in echinoids, accelerated development of the juvenile rudiment relative to the development of larval structures. Similar plastic responses in juvenile versus larval development are seen in echinoid larvae reared on high food levels, which suggests that this plastic response may be related to ingested levels of thyroxine. Furthermore, metamorphosis in the lecithotrophic sand dollar *Peronella japonica* also appears to be dependent on the thyroxine that their nonfeeding larvae can synthesize endogenously. Herein we review thyroxine effects on larval development and metamorphosis in three echinoderm classes, including our (mainly unpublished) data on lecithotrophic and planktotrophic echinoids (several sand dollars [Order Clypeasteroidea] and a few sea urchins [Order Echinoidea]), asteroids (several orders) and a planktotrophic ophiuroid (*Ophiopholis aculeata*, the first report of thyroxine effects in an ophiuroid). We explore the possibility that the ability (or inability) of planktotrophic ancestors to synthesize thyroxine endogenously places constraints on the evolution of lecithotrophy. Such constraints might explain phylogenetic patterns in the transition from planktotrophy to lecithotrophy in echinoderms. We will discuss our results in the context of larval plasticity and life history evolution in echinoderms.

Larval Development, Settlement, and Juvenile Growth of the Sea Cucumber, *Parastichopus parvimensis*.

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The sea cucumber, *Parastichopus parvimensis*, is commercially fished in southern California and Baja California, Mexico; however, little is known about its ecology or reproduction. This study is part of an effort to provide a biological basis for the management of a sustainable sea cucumber fishery in this region. To determine larval development time, settlement substrate preference, and juvenile growth of *P. parvimensis*, we reared *P. parvimensis* from fertilization to the juvenile stage. Cultures were stirred with Plexiglass paddles and fed the marine flagellates *Isochysis galbana* and *Dunaliella teriolecta* every 2–3 d. Twenty-seven days after fertilization, when the larvae had reached the doliolaria stage, we began a settlement preference experiment. Larvae were exposed to a roughened Plexiglass plate with (1) kelp holdfast, (2) rock, or (3) nothing attached. Larvae began settling 28 d after fertilization, and at the conclusion of the experiment, 45 d after fertilization, there was no difference in the number of larvae settled in any of the treatments. As a result of our laboratory study, we would estimate that *P. parvimensis* larvae could settle on various substrates in the field. Juveniles were maintained in the same fashion as larval cultures with the exception that the diatom *Skeletonema costatum* was used as food. Juvenile growth was followed for 1 yr, when juveniles had grown to ~3.5 cm long.

Poster Presentation Abstracts

Comparative Histological and Immunohistochemical Study of Asteroid Tube Foot Adhesion.

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Adhesion in sea stars is the function of specialized structures, the tube feet or podia, which are the external appendages of the water-vascular system. Adhesive secretions allow asteroid tube feet to perform in multiple functions. Indeed, according to the sea star species considered, the tube feet may be involved in locomotion, fixation, feeding, or burrowing. To this variety of functions usually correspond different tube foot shapes. Although the fine structure of asteroid tube feet has been extensively studied, almost nothing is known on the composition of their adhesives. In this study, we have investigated the variability of the composition of sea star adhesive secretions by immunohistochemistry using antibodies raised against the adhesive material of the forcipulatid *Asterias rubens*. The tube feet from 13 sea star species representing five orders and nine families of the Class Asteroidea were examined. The histological study revealed three main tube foot morphotypes—i.e., knob-ending, simple disc-ending, and reinforced disc-ending—that appear to be correlated to species habitat. In immunohistochemistry, on the other hand, the results were very homogeneous. In every species investigated, there was a very strong immunolabeling of the adhesive cells, independently of the taxon considered, of the tube foot morphotype or function, or of the species habitat. This indicates that the adhesives in all the species considered are closely related, probably sharing many identical molecules or, at least many identical epitopes on their constituents.

New Insights into the Functional Role of the Glassy Tubercles and Inter-Tubercular Pores in Seastar *Echinaster (Othilia)*.

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Since their discovery, the functional role of the microscopic transparent protuberances or “glassy tubercles” on the skeletal plates of seastars has remained largely unresolved. Analogous structures can be found in other classes of the Echinodermata, namely the Echinoidea and Ophiuroidea. Previous studies have suggested that in the ophiuroid *Ophiocoma wendti* the combination of the expanded peripheral trabeculae on the dorsal arm plates, underlying nerve bundles and diurnal activity of the chromatophores, function as an additional photoreceptor system. Preliminary evidence from scanning electron microscopy (SEM) and behavioral studies suggests that the glassy tubercles on the skeletal plates of *Echinaster (Othilia)* do not play a functional role as photoreceptors, a utility provided for by the terminal eyespots. Phototactic responses and diurnal behaviors were not observed for changing light intensities or varying substrate colors. SEM of *E. (Othilia)* ossicles revealed the glassy tubercles to be present on both the dorsal and ventral arm plates, the intertubercular pores to be evenly spaced, and the glassy tubercle patch to occupy much of the upper portion of the stereom. These findings are in contrast to the tubercles observed in *O. wendti*. The tubercles found to aid in photoreception are present only on the dorsal arm plates, are found to completely cover the surface of the plate, and occupy a lesser portion of the upper stereom.

Morphological Variation in Three South Atlantic Sea Stars of the Subgenus *Othilia* (Genus *Echinaster*; Family Echinasteridae; Order Spinulosida).

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The Genus *Echinaster* and its subgenus *Othilia* have been the center of systematic controversy for many years. We hypothesize that the problem arises from allelic variation between forms within local populations, and from differing geographic localities. The “species” of *Othilia*: “*brasiliensis*,” “*echinophorus*,” and “*guyanensis*” examined and described in this report were collected from the coast of Brazil

(Pr. Rio de Janeiro northeasterly to Pr. Bahia). Major features examined were gross morphological arm structure, color in life, madreporite and "pentagon" structural features, abactinal plate circling with spines, ocular plate with spination, mouth spines, inter-radial area of the central disk, furrow plates with spines, ventral papular pore series, and inferomarginal plates with spines. *E. Othilia brasiliensis* was found to be scarlet to crimson red to brownish red in life and found on rocks, sand and muddy sand; three "morphotypes" were found. *E. Othilia echinophorus* was found to range in color from dark red, reddish brown, brownish yellow, orange, and bright yellow in life and occurred on sand/shell and low profile rocky coral substrates; two morphotypes were found. Previously described mamiform bases carrying spines may or may not be encountered. *E. Othilia guyanensis* was found in nature to be bright red on top and bottom, and occurred on rocks, sand, and sandy mud; two distinct "morphotypes" were found. The zoogeographic range extends as far south as Guaripari Rocks, Pr. Espirito Santo (north of Pr. Rio de Janeiro).

Reestablishing the Green Sea Urchin in Overharvested Areas.

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The green sea urchin (*Strongylocentrotus droebachiensis*) is the dominant herbivore in benthic, nearshore communities in the Gulf of Maine. Overharvesting of sea urchins has greatly decreased herbivory and produced dense, fleshy macroalgal communities in many areas of western coastal Maine. Macroalgal dominated communities have become stable because grazing has remained low and sea urchins have been unable to reestablish themselves. The latter is due to micropredators that maintain low or no urchin recruitment. This alternate stable state may persist until the feedback loop maintaining the herbivore free conditions can be broken. In order to break this stable state, I have attempted to induce a phase shift by increasing herbivory. In August 2000, 3,000 large urchins were relocated to each of nine sites in Cape Elizabeth, Maine, and all died within 1 mo. Observations of crabs (*Cancer* spp.) preying on urchins in the field led to experimentation in the lab that demonstrated elevated predation in warmer water and on damaged urchins. Another 3,000 large urchins per site were relocated in late April 2001, when crabs were absent and water temperatures were low. On average, there has been <30% mortality since the relocation, and crab abundances have been minimal (<0.1/m²). These data suggest that the vigor of urchins at the time they are encountered by crabs may be very important in attempts to facilitate recovery of sea urchin populations.

Diminutive Ophiuroids of Modern Aspect from the Lower Carboniferous of Nova Scotia, Canada.

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New species A of subfamily Aganasterinae in the family Ophiuridae, new species B of Aganasterinae, and indeterminate species C with distinctive needle-shaped spines were found in carbonates of the Avon Member, Green Oaks Formation, upper Windsor Group, in the Shubenacadie map area of Nova Scotia. The maximum disk diameter is only ~2.5 mm, and the maximum arm length is only ~23 arm segments. This small size is of particular interest because it is consistent with the small size noted overall in the fauna of the upper Windsor Group. An objective of this study was to form an opinion on the most likely explanation for the diminutive size of these ophiuroids.

The strata were deposited in a restricted marine basin with a history of periodic isolation from the sea and with climatic conditions conducive to evaporite deposition. Nevertheless, the ophiuroid fauna was diverse, with three species and abundant with almost 100 individuals. This diversity and abundance suggests a habitable environment for these species (which may be eurytopic). Many extant ophiuroids are of comparable small size.

A growth series leading to character states that look fully differentiated would plausibly differentiate an assemblage that includes diminutive adults from an assemblage composed only of immature specimens. The arm of new species A ($N = 6$) underwent significant morphological changes during growth, and the last growth stage has adult structure, as judged by comparison with growth series in extant ophiuroids. The small size of the fully differentiated individuals tentatively establishes new species A as a naturally small species.

New species B ($N = 89$) grew without significant morphological changes. However, one of the larger specimens of new species B successfully regenerated an arm, showing that the environment was hospitable to "regrowth." This indicates that the small size of new species B is not an artifact of stunted growth. Brooding and viviparity are not uncommon among diminutive ophiuroids. Specimens of *Ophiopyrgus turritus* with a disk diameter of no more than 2.4 mm contain brooded embryos and hence are sexually mature adults. New species B was present in sufficient numbers to speculate that short life span, rapid maturation, and continuous direct recruitment by brooding could account for its small size, population density (1,235 disks) and age structure (growth stages from 0.5 to 2.5 mm disk diameter present). A possible present-day analogue of new species B is the diminutive eurytopic hermaphroditic brooding ophiuroid *Amphiopholis squamata*, which is distributed worldwide, from intertidal to 1,300 m deep, from cold water to the tropics.

Multispecies associations of extant diminutive ophiuroids occur. Therefore, the co-occurrence and congruent small size of these three species is circumstantial evidence that indeterminate species C ($N = 1$) also is a naturally small species.

Ammonia Tolerance of the Sea Urchins *Lytechinus variegatus*, *Arbacia punctulata*, *Strongylocentrotus franciscanus*, and *Paracentrotus lividus*.

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Ammonia is toxic to organisms. Tolerance to ammonia is of basic interest and also has implications for aquaculture. For each species, the sequence of decreasing tolerance is tube feet, Aristotle's lantern and spines. At 12.5 mg $\text{NH}_4\text{Cl l}^{-1}$ (3.25 mg $\text{NH}_4\text{-N l}^{-1}$), the effective time at which the functioning of these organs was reduced 50% (ET_{50}) was >96 hr at for all species. At 25 mg $\text{NH}_4\text{Cl l}^{-1}$ (6.5 mg $\text{NH}_4\text{-N l}^{-1}$), the ET_{50} of the tube feet was ~80 hr for *L. variegatus* and *P. lividus*. Although the tube feet of some *S. franciscanus* and *A. punctulata* were affected at 25 mg $\text{NH}_4\text{Cl l}^{-1}$, the ET_{50} remained >96 hr. Thus the sensitivity to ammonia varies with species. Because the tube feet are very important for the functioning of the individual, their sensitivity to ammonia indicates control of ammonia concentration is essential for aquaculture. Supported in part by Florida Sea Grant to JML.

Production in the Starfish *Luidia clathrata* Measured Directly and Calculated from the Specific Dynamic Action.

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Production, the synthesis of organic matter, is typically measured directly. Specific dynamic action (SDA), the postfeeding increase in metabolic rate, is associated with anabolism and thus associated with production. We tested the prediction that production calculated from the SDA is similar to that measured directly. Long-term production (42 d) was measured directly in *Luidia clathrata* by the increase in proximate constituents of fed individuals and short-term production was measured indirectly by calculation from the increase in oxygen consumption after feeding. The amount of production measured directly (16.2 kJ organic material and 12.8 kJ protein) was much greater than that calculated from the SDA for the equivalent period of time (0.8 kJ). SDA is a useful indicator of specific short-term production but does not adequately indicate actual long-term production.

Allometric Growth of the Asymmetrical Pyramids of the Aristotle's Lantern of the Sand Dollars *Mellita tenuis* and *Dendraster excentricus*.

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The allometric increase in an organ's size has important implications for understanding its development and functioning. In sand dollars, the anterior lateral pyramids (ALP), the posterior lateral

pyramids (PLP), and the posterior pyramid (PP) of the Aristotle lantern of sand dollars increase in size in that order. Pyramids of *M. tenuis* are heavier than those of *D. excentricus* of the same anterior-posterior length. This may be related to differences in food. For both species, pyramid weights are significantly related to body weight but not identically. The slopes of the regressions of pyramid weight to body weight of the ALP = PLP < PP.

Photoperiod, “Eyes” and Gametogenesis in the Green Sea Urchin.

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Shortening fall day-length results in the initiation of changes in two populations of cells within the gonads of both sexes of the green sea urchin, *Strongylocentrotus droebachiensis*. These cellular populations include spermatogonia in males and oogonia in females and somatic cells called nutritive phagocytes (NP) in both sexes. During the summer, gonial cells are amitotic and NP store nutrients; as the photoperiod changes in the fall, gonial cells begin mitosis and NP mobilize nutrients. Details of these processes can be addressed on the web page: <http://zoology.unh.edu/faculty/walker/urchin/gametogenesis.html>. The mechanism for detecting changes in daylength are unknown but might involve tube feet, spines, the dermis, or the gonads themselves. We are using Western blots and immunocytochemistry to determine the expression patterns of PAX6 (the eye master control switch) and rhodopsin proteins within each of these tissues during changes in fall photoperiod (August–October).

It is also unknown whether the response to photoperiod occurs at the level of the NP, which then mobilize nutrients that support gonial cell division, or whether both populations of cells are independently effectors for the photoperiod cue. In order to distinguish between these two possibilities, we are following the expression of the *c-myc* protooncogene and of the SEAWI stem cell master control gene in both males and females in the months when the photoperiod cue is occurring (August–October).

Sea urchin ovaries and testes containing fewer gametes relative to NP are the preferred version of this food in most cultures. Such conditions exist naturally in sea urchins during the summer, and practical applications of this research for aquaculture might result from preventing recognition of changing photoperiod and thus suppressing gametogenesis in the green sea urchin. Gonads in such sea urchins should contain principally or exclusively nutritive phagocytes and would be of superior size, taste, texture, and firmness.

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Weird Science: A Spatangoid Larva (Class Echinoidea, Order Spatangoida) Metamorphoses into a “Typical” Regular Echinoid (Order Echinoidea).

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A swarm of sea urchin larvae was collected in a plankton tow off the Bahamas in October, 1998. The larvae were of the typical spatangoid type (Order Spatangoida), differing from most other echinoid larvae in possessing a well-developed median posterior projection known as the aboral spike, supported by a skeletal calcite rod. Many of the larvae were competent to metamorphose. Approximately 100 individuals were selected, and they completed metamorphosis within 2 hr. Mortality of juvenile echinoids was very high, and over the next 2 wk ~95 individuals died. Two juveniles survived for ~11 mo, and they were fixed in alcohol in September 1999 for further study. Astonishingly, these sea urchins are in the Order Echinoidea, virtually identical to *Echinometra lucunter lucunter* (Linnaeus), and they show no trace of the spatangoid characteristics indicated by the larvae. If the larvae were hybrids, recent research suggests that *Echinometra* eggs were fertilized by spatangoid sperms. However, this hypothesis would require that the phenotype of the larva is determined, at least in part, by the sperm.

Chitin in Echinoderms? Tentacle Sheaths in the Deep-Sea Holothurian *Ceraplectana trachyderma* (Holothuroidea: Molpadiida).

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The eastern Pacific molpadiid holothurian *Ceraplectana trachyderma* H.L. Clark, 1908, was known only from five specimens collected off the Aleutian Islands and off Peru in abyssal depths (3,100–5,200 m). K. Smith (Scripps Institution of Oceanography, San Diego) has collected numerous specimens of this species off central to southern California at ~4,100 m. The body is essentially cylindrical, tapering posteriorly to form a conspicuous tail. The body wall is parchment-like and stiff, due to numerous ossicles and scattered phosphatic deposits. Like other molpadiids, *Ceraplectana* lives buried in the substratum, mouth down, with the tail projecting into the water for purposes of respiration, and it feeds by ingesting quantities of mud. The unique and astonishing characteristic of *Ceraplectana* is that its 10 simple circumoral tentacles are covered by stiff, leathery, conical, dark brown sheaths of unknown function. The structure of the sheaths has been analyzed in a preliminary way, and further analyses are in progress. The sheaths are not proteinaceous; rather, they are composed of a polysaccharide that is very closely similar to the aminated glucose, chitin. Chitin is a very common skeletal element in protostome phyla, but it is extremely rare in deuterostomes as a skeletal element. This may be the first record of chitin in the Echinodermata.

How Many Species of Five-Holed Sand Dollars Live in the Western Atlantic?

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The common Western Atlantic five-holed sand dollar, formerly known as *Mellita quinquesperforata* (Leske), was revised by Harold and Telford (1990). They studied shape of test and lunules, arrangement of basicoronal plates, shape and relative sizes of spines, and relative size of the Aristotle's lantern. Harold and Telford concluded that there are three allopatric species: *M. isometra* n.sp. from the east coast of the United States, *M. tenuis* Clark from the Eastern Gulf of Mexico, and *M. quinquesperforata* from the Western Gulf of Mexico, through the Caribbean to Brazil. DLP studied sand dollars from a depth of 40 m at Capron Shoal, off Fort Pierce, Florida, and found that these individuals seemed to display characters of all three of Harold and Telford's taxa. Further analysis by RJM and DLP of recently collected material from a wider range of localities lends support to Harold and Telford's conclusion that there are indeed three species, but some revision of diagnostic characters is required.

Evidence of Feeding and Digestion in Eviscerated Specimens of an Aspidochirotid Holothuroid.

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The tentacles of *Holothuria* (*Semperothuria*) *cinerascens* (Brandt, 1835), an Indo-West Pacific aspidochirotid holothuroid, common in the shallow waters of the east coast of South Africa, are intermediate between the peltate tentacles characteristic of the order Aspidochirotida and the dendritic tentacles characteristic of the order Dendrochirotida. They are hence best described as "peltodendritic," allowing the species to feed both as a deposit and suspension feeder, and these activities appear to be governed by tidal cycles. In the laboratory at least, eviscerated animals continue to display active tentacular or feeding activity. Histological examination of the foregut remnant of eviscerated animals showed that it seals off after evisceration and its mucosa is lined with villi. Tests for enzymatic activity in this foregut remnant and the remaining respiratory tree of eviscerated animals revealed the presence of protease, amylase, and lipase. All three enzymes were also detected in the foregut and small intestine of noneviscerated animals. It is concluded that eviscerated animals perhaps take in particulate matter from the water column (suspension feeding) and the substratum (deposit feeding) digesting it in the foregut remnant, which thus serves as an effective digestive organ in eviscerated animals. Some digestion may therefore also be possible in the remaining respiratory tree of such specimens.

Alternate Stable States and the Management of the Green Sea Urchin *Strongylocentrotus droebachiensis* in Maine.

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As the only major herbivore, the green sea urchin (*Strongylocentrotus droebachiensis*) is capable of controlling the structure of shallow water benthic communities in the Gulf of Maine. Depletions in urchin populations due to overfishing have resulted in widespread shifts from urchin "barrens" to dense algal beds in the last decade. This transition is rather abrupt once a minimum urchin biomass is reached, and this "threshold" biomass seems to change with both depth and latitude. Recent management measures have created no-take conservation areas along the coast of Maine in an attempt to bring back urchin populations. Research suggests that these populations are not recovering, however, and the algal community shows signs of being extremely stable. Understanding these alternate stable states is important to understanding urchin ecology as well as the appropriate use of management tools such as marine protected areas.

Glucose Levels in the Coelomic Fluid Vary with Diet in the Sea Urchin *Lytechinus variegatus*.

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We hypothesize that glucose has an important role in nutrient translocation in the coelomic fluid of the sea urchin. Previous studies have shown that glucose levels were minimal in several species of sea urchins. The glucose levels in individuals actively consuming a formulated diet (32% protein) had glucose levels of ~30 mg/dL, as determined by Ektachem analysis. After starvation overnight, glucose levels decreased below detection thresholds (<20 mg/dL), which suggests that glucose is translocated from the gut into the coelomic fluid during feeding and removed rapidly into surrounding tissues. In a subsequent experiment, individuals ($n = 9$) fed a low-protein (14%)/high-carbohydrate diet had glucose levels of 55 mg/dL, whereas those individuals ($n = 10$) fed a high-protein (50%)/low-carbohydrate diet had glucose levels below the detection threshold. These data indicate that the level of glucose in the coelomic fluid is directly related to the carbohydrate content of the food consumed. The fate of the glucose is not known, but we suggest that the glucose is incorporated into polymers such as glycogen, particularly in the nutritive phagocytes of the gonadal tissues. Supported in part by Mississippi-Alabama Sea Grant.