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ABSTRACTS OF CONTRIBUTED PAPERS PRESENTED AT THE 1998 NORTH AMERICAN ECHINODERMS MEETING AUGUST 16–19, 1998 WALLOPS ISLAND MARINE SCIENCE CENTER WALLOPS ISLAND, VIRGINIA

In order of presentation

LISTING OF CONTENTS, AUTHORS, AND ABSTRACT TITLES

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FOREWORD

PROCEEDINGS OF THE NORTH AMERICAN ECHINODERMS MEETING 16–19 AUGUST 1998, WALLOPS ISLAND, VIRGINIA

Following the tradition started at the Dauphin Island Sea Lab (1989), and continued at the Harbor Branch Oceanographic Institution (1992), the third North American Echinoderms Meeting was sponsored by the Marine Science Consortium and held at the Wallops Island Marine Science Center in August of 1998. In keeping with the practices of prior meetings, this meeting provided a forum for colleagues from throughout North America to share current work, and fostered communication between researchers whose work is based upon some aspect of the biology of Echinodermata. Presentations covered a range of topics, from evolutionary relationships to ecological processes and from physiological mechanisms to aquacultural applications, illustrating the breadth of activities of researchers investigating the Echinodermata. Following are abstracts resulting from oral or poster presentations contributed to the 1998 North American Echinoderms Meeting, and a special, invited retrospective on meetings on Echinodermata in North America.

ORGANIZING COMMITTEE:

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A History of Meetings on Echinodermata in North America

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One of the major taxa of the world ocean that has been slow to develop a large, devoted following is the Echinodermata. Despite the importance of echinoderms in embryology and development, molecular biology, marine ecology, paleontology, and phylogeny, traditionally their study has been incorporated into these fields rather than into a unified subject. This has had the advantage to students of echinoderms of making them more outward looking than those whose subjects are widely studied such as molluscs and crustaceans. The disadvantage is the converse of course. Echinoderm students are often unaware of pertinent studies outside their horizontal discipline. An indication of coming of maturity of a field is indicated by the origin of meetings specific for that field. It is appropriate that the students in a field be aware of their history. David Nichols (1994) provided an interesting account of the International Echinoderm Conferences at the Atami Conference.

The first meeting devoted to echinoderms in North America was part of the International Congress of Zoology in Washington, DC in 1963. Organized by Richard Boolootian, this meeting brought together eminent echinoderm biologists who covered the field except for paleontology. I was a graduate student at the time and was awed by the participants. I did not have the courage to speak to any of them. This meeting led to the book edited by Boolootian (1966), *Physiology of Echinodermata.*

The first independent meeting on echinoderms in North American was the First International Echinoderm Conference at the Smithsonian Institution in Washington, DC in 1972. As an independent meeting, it had been preceded by a symposium on echinoderms at the Zoological Society of London in 1966. With the exception of Alfred B. Chaet (of the then so-called "shedding substance" of the radial nerves of starfish fame) from the U.S. and E. Pequignat from France (who studied the uptake of organic material by the epithelium of starfish and sea urchins), all participants in this meeting were from Great Britain. Its scope was large and the proceedings were edited by Norman Millott (1967).

David Pawson of the Natural History Museum at the Smithsonian Institution, along with Maureen Downey, was the instigator of the Smithsonian Conference. He recognized that the number of echinoderm students had reached the critical mass for a truly international meeting that could be perpetuated. I remember the call for papers and the follow-up by David who lamented he was finding that hosting an international meeting was more than simply reserving a room and getting a coffee pot. That the latter was insufficient was emphasized in the morning session chaired by Ailsa Clark who announced a recess "for tea . . . , or whatever you call it here." That more was done than just obtaining a room and a coffee pot was obvious in the evening reception in the echinoderm section of the Museum when Maureen opened up some jars of sea cucumbers as treats to accompany the libations provided. I also remember Porter Kier showing a film of spawning *Diadema antillarum.* The spawning was prolonged and we watched bemused for some time until Porter turned to us and exclaimed, "Isn't that *exhausting*?" At the meeting, the participants decided the international conference would be held every 3 yr and the venue would be rotated between the Americas, Europe–Africa, and the East. The participants also recommended that regional meetings be held in the years between the international conferences.

In the interim between the next American international conference, a meeting on echinoderm development as part of the 1973 meeting of the American Society of Zoologists was organized by Fu-Shiang Chia and Arthur H. Whiteley in Houston. The proceedings of this meeting concerned gametogenesis, fertilization, development, and growth were published in the *American Zoologist* (1975). Among those papers I remember best were those of Gordon Hendler on ophiuroid development, of Thomas Ebert on echinoid life histories, and of John and Vicki Pearse on echinoid growth lines.

The Tampa Bay International Echinoderms Conference in 1981 almost did not happen. The Third International Conference was in Sydney, Australia. As David Nichols (1994) noted, the distance was such that the number of participants was understandably small. Consequently, no decision was made regarding the subsequent conference. In spring 1980, as I had received no information about the conference due in 1981, I called David Pawson to en-

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quire. He informed me that none was scheduled. As he and I both felt the importance of continuing the now 9-yr-old tradition, we communicated with a number of individuals in the Americas asking if any would be able to organize the conference. None were. As I had benefitted from the hospitality of friends and colleagues at other meetings, I told David I would host the conference. Such was the basis for the Fourth International Conference held in a seaside hotel on the beach of the Gulf of Mexico at the mouth of Tampa Bay. I was fortunate to have the assistance of four graduate students from my laboratory: Walter Diehl, Adam Marsh, James McClintock, and Stephen Watts. I was convinced that each conference should provide for the next and that an invitation should be guaranteed. As the rotation of venue indicated the Fifth Conference should be in Europe–Africa, I looked at the places there I had not had the fortune to visit and thought Ireland might be fun. I had met Brendan Keegan at the Second Conference at Rovinj, Yugoslavia. Barely, as he and the rest of the Irish contingent had spent most of their time in Venice obtaining permission to enter and arrived only at the very end. Brendan was enthusiastic about hosting the conference and made arrangements for one of his students, John Costelloe, at the Skidaway Institution at that time to tender an invitation.

The Sixth International Conference was held in British Columbia in 1987. No host was available in the East for that year and the participants at the Galway Conference in 1984 had rationalized that the longitude of Victoria was sufficiently close to the East to qualify. Robert Burke organized the Victoria Conference on the beautiful campus of the University of Victoria. Subsequent conferences resumed their itinerary via Atami (1990) and Dijon (1993) before returning to the Americas for the Ninth International Conference, the San Francisco Conference organized by Richard Mooi of the California Academy of Sciences. Among the notable events here were the number of visitors who did not know that ". . . San Francisco, it's cold and it's damp!" With the normal progression, the next International Echinoderm Conference will be in the Americas in 2005. A movement of the venue south to the Caribbean or South America should be considered.

Regional meetings have been held intermittently between the International Conferences. Designed to be more informal and to promote interaction to a greater extent than possible at them, the first regional meeting of the Friends of Echinoderms was at Dauphin Island, Alabama in 1989, organized by Thomas Hopkins, James McClintock, and Stephen Watts. A second was at Harbor Branch Oceanographic Institute, Fort Pierce, Florida in 1992, organized by Sid Bosch and Craig Young. I remember Dan Blake commenting that he didn't recognize half the participants and Fred Hotchkiss responding, "That's because half are under thirty!" The high degree of participation by young investigators is one of the most valuable aspects of these regional meetings. This is the third, perhaps now more respectfully titled, North American Echinoderms Conference, organized by Thomas Klinger. On an even smaller scale is the Florida Echinoderm Festival. Its roots go back to 1972, when I and two of my graduate students (Pam Prim and Ross Ellington) and Stephen Stancyk and John Caldwell, then graduate students at the University of Florida, met one Saturday at the University of Florida Marine Laboratory at Seahorse Key to tell each other about our work. This was made regular when the First Festival that was hosted by Larry McEdward at the University of Florida in 1995, followed by the Second at Eckerd College hosted by John Ferguson, and the Third at Jacksonville University in 1998. The Fourth will be at the University of South Florida in 1999.

Two other traditions of echinoderm meetings must be noted. One has resulted from the conspicuous role of echinoderms in geology. Two specific sessions on echinoderms have been part of meetings of the Paleontological Society and have led to publications by the society (Broadhead and Waters, 1980; Waters and Maples, 1997). In the latter, Lane (1997) gives a history of the geological "Friends of Echinoderms," an account of the tradition of informal evenings at the annual meeting of the Geological Society of America that began in 1966. These were initiated and hosted by Gary Lane and then by Ron Parsley. Similar evenings of echinoderm friends occurred at the annual meeting of the American Society of Zoologists in the 1970s. I remember particularly the meeting at Philadelphia when Gordon Hendler and I had to carry large, brown paper bags over several city blocks back to the hotel.

A final tradition of echinoderm meetings in the Americas is just developing: fisheries and aquaculture of echinoderms. A number of years ago, my dean wandered into my laboratory, saw my aquaria with sea urchins, and told me, "John, you should be working with lobsters." I told him I didn't want to work with lobsters; they had too many legs and did disgusting things like molting. Although sea ur-

chins have been eaten since prehistoric times in the northwest of North America, the Caribbean, and the west coast of South America, their contemporary use is primarily in Barbados and Chile. Recently, however, North Americans have discovered to their amazement that sea urchins are a delicacy in much of the world and, as other fisheries have become overfished, have determined that sea urchins in their turn should take their place for exploitation. Thus, meetings have been organized to consider fisheries and management and, as this potential has been seen to be insufficient, to aquaculture as well. These meetings have been in Canada (Pringle et al., 1980; Aquaculture Canada '96), California (Anonymous, 1992), and the northeast U.S. (Anonymous, 1995). A session on aquaculture of sea urchins and sea cucumbers was part of the San Francisco Conference. But that it had finally arrived was apparent when Charles Walker and Michael Lesser organized a session on sea urchin aquaculture for the International Triennial Conference and Exposition on Aquaculture in Las Vegas in 1998 with the proceedings to be published in *The Shellfish Journal.* Lesser pointed out that sea urchins qualified for the journal by virtue of their test.

It is fit and meet that coworkers in a field meet periodically to discuss their work and to establish acquaintances and friendships. The goals of professional development and personal pleasure are not mutually exclusive as evidence by meetings such as these.

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ABSTRACTS

Regeneration of Arms in *Luidia clathrata* (Echinodermata: Asteroidea) in the Field, Tampa Bay, Florida

CHRISTOPHER M. POMORY AND MICHAEL T. LARES

In a survey of the population (n = 1,957), 41% were not regenerating, 16% were regenerating one and two arms, respectively, 15% were regenerating three arms, and 6% were regenerating four and five arms, respectively. Individuals for a manipulative experiment had two adjacent arms removed at the disk edge. Experimental "cohorts" were cut and released in September 1996, November 1996, March 1997, and October 1997 in upper Tampa Bay, Florida. Follow-up collections were made at 2-mo intervals. Since the experimental method represented a mark and recapture technique, the Lincon–Peterson index was used to calculate population size at several times of the year and produced an average estimate of approximately 68,000. Regeneration of two arms takes 380 days based on regression equations. Regeneration of length is initially faster than dry mass. Both arms within an individual regenerate at the same rate based on length or dry mass. The regression equation for length is Y = sqrt(25.968X) and for dry mass is Y = 0.259X, where Y is the percentage of a whole arm and X is days. There was no difference in gonad, pyloric ceca, or body wall dry weight of a nonregenerating arm compared between regenerating and nonregenerating individuals; however, sample size and thus power of the statistical tests were low.

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Variations in the Distribution and Abundance of *Lytechinus variegatus* in Saint Andrew Bay, Northern Gulf of Mexico

S. ANNE BOETTGER, STEPHEN A. WATTS, JAMES B. MCCLINTOCK, LARRY E. THOMPSON, AND JOHN M. LAWRENCE

The distribution and abundance of *Lytechinus variegatus* were measured at three shallow water (1–1.7 m) sites in St. Andrew Bay in the Northern Gulf of Mexico. All study sites had dense populations of the turtle grass *Thalassia testudinum.* Populations were monitored in August and November of 1997, and April and July of 1998, and a significant mortality event was observed in April 1998. Animals were measured (mm) along a 2 × 10-m transect, with four transects per site. Observations on the abundance of *T. testudinum,* water salinity and temperature were recorded. The results were examined statistically in a Pearson chi-squared contingency table ($P < 0.05$). In August 1997 individuals ranged in size from 15 to 63 mm (mean = 38 mm) in diameter at Station 1 (Station 2 and 3 were not sampled). By November 1997 individuals at Station 1 ranged in size from 26 to 62 mm (mean = 48 mm), suggesting the population grew rapidly. Population densities were estimated at 0.6 individuals/m^2 in November. Individuals at Station 2 ranged between 50 to 70 mm (mean = 59 mm), indicating that this population had received no recent recruits. At Station 3, individuals ranged between 36 to 70 mm (mean = 51 mm) in size. Salinities were 31–32 ppt at all stations. In April 1998 salinities had dropped to 18–24 ppt due to the unusually high spring rainfall and only individuals ranging from 22 to 33 mm (mean = 29 mm) were found at Station 3 (24 ppt). Large numbers of dead individuals and tests were found along the shoreline of Stations 1 and 2 with test diameters ranging from 20 to 75 mm with densities as high as 45 individuals/m^2. By July 1998 individuals were still not observed at Station 1. Individuals reappeared at Station 2, ranging from 28 to 55 mm (mean = 41 mm); however, densities had decreased from 1.05 to 0.6 individuals/m^2 from the November collection. At Station 3 individual sizes ranged from 20 to 47 mm (mean = 38 mm), but densities decreased from 1.55 to 0.3 individuals/m^2. The differences in the survival of animals at the different stations may be due to the water currents within the bay. This research is supported by Mississippi–Alabama Sea Grant.

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Is the Labidiasteridae (Forcipulatacea: Asteroidea) Paraphyletic?

CHRISTOPHER MAH

The Labidiasteridae Verrill, 1914, is an assemblage of multiarmed asteroids found throughout the world's oceans. It currently includes *Labidiaster, Coronaster, Rathbunaster,* and *Plazaster.* Most species are deep-water with some shallower water representatives. Although, historically known as an "unnatural" or paraphyletic assemblage, little has been undertaken to disprove monophyly of the Labidiasteridae. Although a phylogeny of the forcipulatacean clade is a necessity for demonstrating paraphyly, an examination of the characters reveals an absence of well-defined synapomorphies, casting doubt on the validity of the Labidiasteridae. The following includes characters from Clark and Downey (1992) and W. K. Fisher reinterpreted within a phylogenetic context. Parallel development of multiple arms in different forcipulatacean clades (e.g., the Brisingida, the Asteriidae, the Heliasteridae) suggests this character would have little value as a synapomorphy in this context. Some characters traditionally used to define the Labidiasteridae are found in other asteriid taxa and may represent either potential synapomorphies with non-labidiasterid asteriids or plesiomorphies within the forcipulatacean clade. For example, scattered abactinal plates in a fleshy body wall and an absence of actinal plates suggests a relationship between *Rathbunaster californicus* Fisher, from the Pacific Northwest, with pycnopodiine asteriids (such as *Pycnopodia* and *Lysasterias*). Biserial tube feet are found in the sister group to the forcipulatidan clade and could be considered plesiomorphic. Placement of *Plazaster borealis* (Uchida) within the Labidiasteridae is questionable due to a lack of any distinct characters shared with the other taxa, including the presence of a single, prominent, inferomarginal spine. An internal, dorsoventral, interradial, pillar on the oral disc, found in *Coronaster, Labidiaster,* and *Plazaster* and is shared with *Psalidaster* and the coscinasterine asteriids. This character was dismissed by Fisher (1941) as a convergence but should be reconsidered as a possible synapomorphy for these taxa in a phylogeny of the forcipulatidans. Given the potential for convergence within the forcipulatidans, a revision is a daunting task.

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Status of the Genera in the Ophiuroid Family Ophiolepididae: Time to Take out the Trash?

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Though well over 2,000 species have been described, the Ophiuroidea have never been properly monographed. It is not surprising therefore that there are problems in coding and defining characters for the families. The current classification of the group is based on a regional fauna and as such is limited. Previous authors rarely diagrammed complete specimens, and those that were shown were often atypical forms. The diversity of the families is usually not adequately represented. Later culling of these works for character coding in cladistic analyses is restrictive and new sources of character data are needed. The families must be revised and their characters identified by examination of the genera that comprise them. This work is a summary of initial findings concerning the validity of the 15 genera in the Ophiolepididae. This family is often diagnosed by the presence of thick plates covering the disk and the second oral tentacle pores opening inside the jaw angles. This study indicates that these alone are unsatisfactory characteristics. All ophiuroids possess naked disk plates at some point in their development, prior to the formation of secondary ornamentation like granules. The second oral tentacle pore opens within the jaw angles in many families. The Ophiolepididae has become a "trash can" for genera with naked disk plating, including juvenile forms of other families. This study finds that the genus *Ophiomidas* is a juvenile *Bathypectinura* (Ophiodermatidae). *Amphipholizona* is transferred to the Amphiuridae, though it may represent a juvenile of a known form. *Ophiosphalma* and *Ophiolipus* are identified as likely synonyms of *Ophiomusium. Ophiolebella* is synonymized with *Ophiolebes* (Ophiacanthidae). The placement of *Ophiopenia* within the Ophiolepididae is questioned. *Ophioplocus januarii* and *O. declinans* are transferred to *Ophiozonoida,* and the genus *Ophioplocus* is restricted to include only forms with moderate to extensive "fragmentation" of the dorsal arm plates.

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The Tagmatized Echinoderm

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Tagmosis is a derived condition of metamerism in annelids, arthropods, and chordates in which groups of adjacent segments are modified to perform specific functions. Examples are the clitellum of earthworms, the carapace of lobsters, and the sacrum of tetrapods, to mention a few of many. Examples of tagmosis are not hard to find among echinoderms, a fourth major phylum of metamerized animals; but the degree of tagmosis is weak in most cases. The first few elements of the axial skeleton are often fused as special structures (jaws and other parts of the oral frame, lantern supports) in asteroids, echinoids, and ophiuroids. Crinoid pinnules occur in groups along the arms as genital pinnules and oral pinnules. Porcellanasterid seastars have cribriform organs along the marginal plates for generation of respiratory currents. Well-developed podial pores and podia are restricted to basal segments of the ophiuroid genus *Ophiomusium*. Ambulacral plates of most post-Paleozoic echinoids occur in clusters that result in arcs of pore pairs and in the compound formation of spine tubercles, giving rise to several non-cidaroid tagmatized patterns. The strongest degree of tagmosis occurs in the bilaterally symmetrical echinoids, with petals, phyllodes, plastrons, and frontal ambulacra; and tagmosis differs among the axes. Tagmosis is poorest in holothuroids, bodies of which are almost entirely composed of extra-axial elements.

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Molecular Phylogeny of the Forcipulatida (Asteroidea)

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The Forcipulatida, composed of the families Asteriidae, Heliasteridae, Zoroasteridae, Pedicellasteridae, Labidiasteridae, and Neomorphasteridae, contains many species with variable morphologies. Because of this variability, phylogenetic relationships within the Forcipulatida have been difficult to determine using morphological characters. The Asteriidae is a particularly problematic group because of its large size (containing the majority of forcipulatidan species). Fisher (1928) regarded the Asteriidae as a "polyphyletic aggregation of genera" and chose to divide it into subfamilies. Today, three of these subfamilies are recognized, the Asteriinae, Coscinasteriinae, and Pycnopodiinae. However, there has not been conclusive evidence supporting monophyly of the Asteriidae, and a robust phylogeny of the Forcipulatida has not been proposed. A molecular phylogeny of the Forcipulatida is presented here. This phylogeny, produced from an analysis of DNA sequences of mitochondrial tRNAs and the COI gene, provides an alternative assessment of forcipulatidan relationships without relying on morphological characters that often have confounding variability. All subfamilies of the Asteriidae as well as the Heliasteridae and Labidiasteridae are represented. A species in the genus *Brisingaster* (Brisingida) is used for out-group comparison. Analyses indicate that the asteriid subfamilies are not natural groups and that the labidiasterid, *Rathbunaster californicus* falls within the asteriid clade. This phylogeny is not reflected by the present taxonomy of the Forcipulatida. Further studies of this group are warranted.

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Effects of UV Light on Echinoderm Development During the Antarctic Springtime Depletion of Ozone

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Losses of stratospheric ozone over Antarctica have brought increases in the intensities of biologically harmful UVB radiation entering the ocean during the austral spring. This is a time when embryos and larvae of the sea star *Psilaster charcoti* and the sea urchin *Sterechinus neumayeri* develop in surface waters. Experimental exposures of eggs and early cleavage embryos to ambient UVB in outdoor tanks and from the surface to 7-m depths in the water column resulted in significant damage compared to treatments without UVB and to dark controls. In addition to mortality, a variety of nonlethal effects were observed, including DNA damage, disruption of mesenchyme function, occlusion of the blastocoel, reduction of blastula size, and delay of development. Overall, the success of development to

a normal blastula stage in both species was inversely related to the total calculated ambient UVB dose. Under normal ozone conditions, UVB effects on embryos were detected to a depth of 1–3 m. With a depleted ozone column, damage occurred to depths of 5–7 m. UVB light may be detrimental to the early survival of *P. charcoti* and *S. neumayeri*. The extent of mortality and developmental damage might depend on the timing of spawning and the residence times of eggs and embryos in the top few meters of the water column.

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The Chemical Ecology of Antarctic Echinoderms

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Our investigations have revealed that predatory sea stars and sea urchins are likely to have had an important role in the evolution of chemical defenses among Antarctic sessile and sluggish marine invertebrates and macroalgae. A wide variety of sponge, soft coral, and gastropod chemical deterrents causing tube-foot retractions or rejection of artificial foods from the ambulacral groove have been documented in sea stars, while crude extracts of two species of red algae inhibit phagostimulation in sea urchins. Antarctic echinoderms may also employ chemical defenses to protect themselves. For example, we have found the eggs, embryos, and larvae of three lecithotrophic sea stars to be unpalatable to sympatric predators, while the planktotrophic eggs and larvae of a sea urchin and sea star are palatable. Moreover, the sea star *Acodontaster conspicuus* may employ steroid oligoglycosides and polyhydroxysteroids as antifoulants against sympatric Antarctic microbes. Eighteen of these compounds were evaluated for their ability to inhibit growth in Antarctic marine bacteria isolated for either the water column or the surfaces of Antarctic benthic marine invertebrates. Of these compounds, 50% were active against at least one Antarctic marine bacterium. Supported by grants to JBM and BJB from the NSF. This paper is dedicated to the memory of Professor Luigi Minale.

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Inhibition of Algal Spore Settlement Caused by Aqueous and Organic Extracts of Seastar Body Walls

STEPHEN P. GREER, CHARLES D. AMSLER, AND JAMES B. MCCLINTOCK

Luidia clathrata and many other Gulf of Mexico sea stars are rarely observed to be overgrown by fouling organisms. Previous biological and biochemical analyses of this phenomenon has led to the discovery of various bioactive compounds which inhibit settlement and subsequent biofouling by invertebrate larvae and marine bacteria. The initial settlement of marine algal spores is also known to contribute significantly to the biofouling of substrates. Here we show that bioactive compounds found within aqueous and acetone extracts of *L. clathrata* body walls significantly inhibit *Ectocarpus siliculosus* spore settlement. Further characterization of these and other Gulf of Mexico sea star body wall compounds may provide effective alternatives to current antifouling technologies that rely heavily on controlled release of broad-spectrum toxins from metal-based paints.

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How Do Echinoderms Maintain Fluid Balance?

JOHN C. FERGUSON

Echinoderms have an obvious need to maintain fluid in their usually spacious body cavities. Most other animals maintain fluid balance primarily by osmotic uptake of water through the gut or directly through the integument and adjust ion or water levels with excretory structures. Echinoderms, how-

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ever, are usually thought to lack such requisites, although they do possess a hydropore or madreporite that questionably could provide an unusual route for fluid uptake. A series of studies on different types now provides insight into this puzzle. They indicate that a variety of mechanisms contribute to water balance, with several often being important in any given species. Indeed, a major explanation for the diversity of echinoderm body forms may be found in the balance of strategies that are emphasized by different groups. It has been found that all these animals are really slightly hyperosmotic and thus can take up some water directly, that the madreporite system pumps water into the body for the benefit of all regions (not just water vascular system), and that physical (hydrostatic) uptake of water through the mouth, anus, or other parts can play an important role in diverse species. Most notably, the flexible fluid-filled bodies of asteroids are made possible by the supplement of relatively large volumes of water filtering through the Tiedemann's bodies from the madreporite and stone canal. Ophiuroids have reduced coelomic spaces and positive pressures in their genital bursa and thus only have a minimal hydropore system that provides small additional amounts of fluid primarily to the water vascular channels. Echinoids rely on a rigid test that not only fixes fluid volume but also allows a negative net hydrostatic pressure to develop in the body cavity by action of the lantern, which draws in water reducing the need for madreporitic influx. Holothuroids undoubtedly gain water through hydrostatic pumping of their rectum and thus use their internal madreporite to distribute fluid to their water vascular system and to maintain an internal circulation and filtration that is probably common to all echinoderms. No data are yet available on crinoids.

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Limits to Salinity Tolerance of the Brackish-Water Brittlestar *Ophiophragmus filograneus*

RICHARD L. TURNER AND JANELLE A. WOOD

Previous studies on salinity tolerance of the infaunal amphiurid brittlestar *Ophiophragmus filograneus* from Florida coastal waters have documented its ability to acclimate to a wide range of salinities under acute and gradual exposure in the laboratory (ambient salinities 21–25 ppt). Acclimatization to short-term natural reduction in salinity has also been demonstrated (ambient salinity 17 ppt). In all cases, salinities below 10 ppt were lethal within a few weeks of exposure. Recent long-term changes in hydrology have exposed a dense (163/s m^2) population of *O. filograneus* in the Banana River Lagoon to 1 yr (1995) of salinities between 15 and 20 ppt and 2 yr (1996–1997) below 15 ppt. The burrowing response of these animals subjected to acute exposure was tested in the present study at salinities of 8, 10, 12, 14 (ambient), 19, and 24 ppt. After almost 6 wk of continuous exposure, animals at 19 and 24 ppt had fully acclimated. Burrowing times of animals at ambient (14 ppt) salinity were similar to times of animals held at higher ambient salinities in previous studies. Those at 12 ppt still had elevated burrowing times. Animals at 10 ppt survived, but many did not burrow within the allotted time (7 min) for each trial. None at 8 ppt burrowed nor survived more than 15 d. Long-term (3 yr) exposure to low salinity does not seem to extend the tolerance of *O. filograneus*: it has a lower lethal limit of about 8–10 ppt. Although brittlestar population densities at the study site presently are within the range of values reported over the past 16 yr, poor management of surface water runoff to coastal waters in Florida might produce local extinctions of this brittlestar.

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The Effects of Declining PO_2 and Hypercapnia on the Oxygen Consumption Rate of *Hemipholis elongata* (Echinodermata: Ophiuroidea)

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Hemipholis elongata is a burrowing ophiuroid that is believed to utilize hemoglobin for oxygen transport via the water vascular system. It maintains a constant oxygen consumption rate of 0.039 ml O_2 g^{-1} h^{-1} ± 0.007 ml O_2 g^{-1} h^{-1} (mean ± SD, n = 10) down to a PO_2 of 22.3 mm Hg ± 5.3 mm Hg. Below this critical PO_2, the oxygen consumption drops to 64% of the previous rate (0.025 ml O_2 g^{-1} h^{-1} ± 0.003 ml O_2 g^{-1} h^{-1}). Oxygen consumption continues until all measurable oxygen is depleted. Animals exposed to hypercapnia (high carbon dioxide; PCO_2 = 15 mm Hg) maintained a constant oxygen consumption rate of 0.034 ml O_2 g^{-1} h^{-1} ± 0.007 ml O_2 g^{-1} h^{-1} (n = 14) down to a PO_2 of 26.9 mm

Hg ± 6.2 mm Hg. The oxygen consumption rate then drops to 67.6% of the previous rate. These results indicate that the response of *Hemipholis elongata* to declining PO_2 is unaffected by hypercapnia, both in oxygen consumption rate and critical PO_2. These results also suggest that the hemoglobin is insensitive to high levels of carbon dioxide.

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Microhabitats of Co-occurring *Lytechinus variegatus* and *Arbacia punctulata* (Echinodermata: Echinoidea) on the Florida Gulf Shelf

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The Hourglass Cruises showed *Lytechinus variegatus* and *Arbacia punctulata* co-occur on the Florida Gulf coast shelf. As the two species differ greatly in their morphology, their co-occurrence is of interest in terms of their ecological requirements and biology. Both species occur at Caspersen Beach near Venice (27°07'N, 82°27'W) ~400 m offshore at a depth of 7 m on limestone rubble covered with algae. *L. variegatus* also occurs on surrounding sand. In September–October 1997 the density of *L. variegatus* on the rubble was 0.18 ind m^{-2} and that of *A. punctulata* was 0.22 ind m^{-2}. Both species also occur at 28°07.56'N, 82°59.70'W west of Egmont Key at a depth of 15 m. There, *A. punctulata* occurred only on rocky outcroppings while *L. variegatus* occurred only on the surrounding sand and rubble. In September 1997, the density of *L. variegatus* was 1 ind m^{-2} and that of *A. punctulata* was 0.33 ind m^{-2}. In February 1998 the density of *L. variegatus* was 0.76 ind m^{-2} and that of *A. punctulata* was 1.19 ind m^{-2}. These differences in microhabitats may reflect differences in preferences. Differences in biology (such as size and gonadal development) may be associated with these differences in microhabitat. The Egmont population of *A. punctulata* had a significantly greater Aristotle's lantern index and a significantly smaller gut index compared to the Caspersen population. In February 1998 this population of *A. punctulata* was compared to another of similarly sized individuals found nearby (28°08.56'N, 83°08.82'W) at a similar depth. No *L. variegatus* occurred at the second site. The Aristotle's lantern index of the first population of *A. punctulata* was significantly larger than that of the other while the gonad index was smaller. Both index differences suggest food limitation for the first population as one would expect a relatively larger Aristotle's lantern index and smaller gonad index with less food. We thank the Florida Institute of Oceanography for ship time on the RV Bellows and its crew for their invaluable help.

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Origin of Abnormal Numbers of Rays in Starfish (Echinodermata)

FREDERICK H. C. HOTCHKISS AND JOHN M. LAWRENCE

Although starfish with an abnormal number of arms have long been known, analysis of the abnormality is rarely done. As most species of starfish have five arms, most abnormalities involve individuals having either four or six arms. In some cases, these individuals show evidence of having been five-rayed originally with the abnormal arm number resulting from injury and repair or regeneration. Interpretation of the origin of very regular four-rayed and six-rayed individuals of normally five-rayed species for which no evidence of injury is evident is speculative. The etiologies inferred for abnormal individuals of normally five-rayed starfish parallel those for fissiparous starfish (e.g., *Coscinasterias*) and multiradiate starfish that intercalate rays after metamorphosis (e.g., *Heliaster*).

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The Sea Urchin *Tripneustes depressus*, the Sea Cucumber *Selenkothuria theeli*, and the Starfish *Phataria unifasialis* (Echinodermata) at Punta Los Frailes and Punta Carnero (Ecuador)

JOHN M. LAWRENCE AND JORGE SONNENHOLZNER

Tripneustes depressus and *Phataria unifasialis* were found together on rubble in a protected embayment on the west side of Punta Los Frailes (PLF) while *Selenkothuria theeli* was found in crevices on a rock

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bottom at the east tip of the point and in tide pools of the rocky intertidal at Punta Carnero (PC). Eighty percent of the *T. depressus* had a test diameter of 91–110 mm with a 1% cohort of 66–70 mm. Sixty percent of the *P. unifasialis* had an arm radius of 61–70 mm with cohorts of 10% at 76–80 and 2% at 91–95 mm. *Selenkothuria theeli* at PC had body lengths ranging from 45 to 135 mm, with 92% > 70 mm while those at PLF had body lengths ranging from 50 to 100 mm, with 85% > 70 mm. The incidence of arm loss in *P. unifascialis* and of body regeneration in *S. theeli* were <5%.

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Eccentricity of the Apical System and Peristome of Sand Dollars (Echinodermata: Echinoidea)

JOHN M. LAWRENCE, CHRISTOPHER M. POMORY, AND BORIS WAWRIK

Eccentricity is associated with directional movement. Although sand dollars have directional movement, only eccentricity of the anus is apparent. That of the apical system and peristome is not. However, paleontologists and taxonomists have often noted and occasionally documented "slight" eccentricity of these structures. The apical system and peristome are statistically significantly anterior in *Mellita tenuis, M. quinquiesperforata, M. isometra,* and *Encope aberrans.* The peristome of *Leodia sexiesperforata* is central and that of *Echinarachnius parma* is anterior, while the apical system of both are posterior. The usual selective pressure for anterior displacement of the mouth in animals with directional movement may be countered by the feeding system of sand dollars. The basis for the eccentricity of the apical system is not known.

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Variation in Tubefoot Structure Along the Length of a Burrowing Brittlestar *Acrocnida brachiata*

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Acrocnida brachiata (Montagu) is a burrowing ophiuroid with a discontinuous distribution throughout the coastal waters of North West Europe. It is found sublittorally to 40 m (Mortensen, 1927) in clean fine sand (Keegan et al., 1985) in burrows approximately 10 cm deep. *Acrocnida brachiata* has arms up to 15 times the disc diameter (Montagu, 1804). Tubefeet in ophiuroids vary by species, as they are adapted to different functions (McKenzie, 1985; Woodley, 1980). However, variation of tubefoot structure within an organism has not been studied. Electron microscopy and histological studies were used to observe variation in the tubefeet of *A. brachiata* from the arm tip to the disc. All tubefeet had a large terminal knob similar to that described in *Ophiocomina* (McKenzie, 1985). At the distal end of an arm tubefeet decreased in size. Prior to this they were covered in large papillae. The number and size of these tubefoot papillae decreased toward the proximal end of the arm. With the reduction in papillae, a single large mucus gland was apparent at the base of each proximal tubefoot. Both the papillae and the mucus gland contained goblet cells (Buchanan, 1962). The mucus gland was found to produce both acid and neutral mucopolysaccharides. This variation in tubefoot structure is thought to be related to burrow maintenance and feeding strategies.

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What is "Local Degeneration" in Holothurian Body Wall?

ROBERT B. HILL

What is "local degeneration" in holothurian body wall? Is liquefaction different from the widely studied relaxation or softening? Crozier (1916) first used the term "local degeneration" to describe the softening induced by mechanical pressure in the body wall of *Isostichopus badionotus* the "sea pudding" (SP). Since then, rapid local degeneration (LD) has been familiar to anyone who has handled living sea cucumbers of that species at the Bermuda Biological Station (BBS). In the course

of minutes, the major part of the initially firm body wall flows out in a sticky mass. This appears to be physiologically triggered rapid tissue self-destruction, which is quite different from the phenomenon of echinoderm tissues plasticized and stiffened under calcium control. Work at the BBS, communicated by W. R. Ellington, showed that collagenase is present in SP body wall tissue and that collagen breakdown increased during LD. Specimens of the SP, collected at the BBS, were kept in the URI Research Aquarium for experiments on LD. Samples of ooze were analyzed by F. Rahemtulla at UAB. The amino acid composition of the ooze produced in LD resembled that of proteoglycans from mammalian tissue, being rich in aspartic acid, glutamic acid, glycine, serine, alanine, and leucine. Immunodetection, gel electrophoresis, and gelation zymography confirm the release of proteoglycans in LD of SP body wall. The proteoglycans absorb water and form the mucinous ooze, which is characteristic of LD. Specimens of the SP were taken to the BioCurrents Research Center at the MBL in Woods Hole. In a preliminary experiment with the self-referencing calcium probe, mechanical stimulation led to an immediate large inward calcium current at the epithelial surface of a segment of body wall. With time, LD set in and the inward calcium current gave way to an outward calcium current that may be due to loss of tissue integrity. We hypothesize that pressure induces a massive cellular influx of calcium, which leads to activation of latent collagenases, releasing proteoglycans. Tests with manual mechanical pressure, carried out at the BBS, have established that four antioxidants are effective in blocking LD in cubes cut from SP body wall: ethyl gallate, propylene phenoxetol, BHA, and propyl gallate. They are hypothesized to block a step in which reactive oxygen species mobilize a cascade of intracellular reactions.

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Chemosensory Search Behavior in the Starfish *Asterias forbesi*

JONATHAN DALE

Starfish use chemoreception to locate odor sources but their orientation strategy has not been well studied nor have their orientation paths in turbulent odor plumes been analyzed. I observed orienting starfish in a large (12-m) flume and examined their orientation paths to determine what types of strategy they could be using. Starfish that moved to the odor source showed low mean heading angles and significant decreases in heading angle as they approached the source. In contrast to control starfish that were presented with no odor, orienting starfish also moved more slowly and did not increase in speed significantly over the course of trials. Control starfish moved more quickly and in all directions relative to flow, rather than moving consistently upstream or cross stream as has been reported in the literature. These results are consistent with a chemotactic orientation strategy and not with a strategy of chemically gated rheotaxis. Plume concentration measurements indicate that comparison of mean concentration between rays is a viable orientation strategy for starfish but not for other benthic predators with higher movement speeds. Prior lesion experiments suggest that turning decisions during orientation occur through a process of competitive inhibition between rays, and an orientation model based on that conclusion is both consistent with the present results and reliable at reaching a simulated odor source.

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Manipulation of Food and Photoperiod Promotes Out-of-Season Gametogenesis in the Green Sea Urchin, *Strongylocentrotus droebachiensis*: Implications for Land-Based Aquaculture

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We have produced green sea urchins (*Strongylocentrotus droebachiensis* O. F. Müller) in which gametogenesis and large gonad size occurred earlier in the year than normal. This was accomplished by providing urchins with an abundant supply of pelletized food prior to and during gametogenesis and by premature exposure to autumn photoperiod. Urchins were collected in February 1995 from New Hampshire waters and were maintained for 7 mo in a land-based facility under artificial illumination. For the first 2 mo, urchins were held under summer photoperiod and were fed a commercially available food. These urchins showed a significant increase in the size of their gonads (gonad index, GI > 25%) compared with urchins collected concurrently from the field (GI = 10–15%). Stereological

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and histological examination of gonads during this time indicated that the increase in size resulted from growth of nutritive phagocytes, which are somatic nutrient storage cells in the germinal epithelium. Spermatogonial or oogonial mitoses were not observed. Urchins fed in this way were then exposed to autumn photoperiod, an environmental cue correlated with initiation of gametogenesis in many shallow-water echinoderms. In male urchins, spermatogonial mitosis and normal spermatogenesis occurred prematurely. In female urchins, oogonial mitosis and subsequent vitellogenesis also occurred prematurely, although resulting primary oocytes did not reach full size. In experimental urchins of both sexes, growth of nutritive phagocytes and gametogenesis resulted in gonad indices of 25–30%. Throughout this study, there was no significant increase in the size of the test of any experimental urchin. This is the first study to couple experimental manipulation of reproduction in sea urchins with stereological and histological analysis of gametogenesis. Our results show that green sea urchins fed an abundant supply of food and treated prematurely with autumn photoperiod, will initiate gonial cell mitosis and will undergo an additional gametogenic cycle in the same year. A comparable study was conducted in 1997 and produced similar results. However, the second experiment compared gonad index and histology of gametogenesis to assess more accurately urchin reproductive state. Monthly observations of resin-embedded gonad samples contribute important details of the reproductive cycle of the green sea urchin not available from gonad index alone. We discuss the implications of our results to understanding sea urchin gametogenesis and also to land-based aquaculture of the green and other sea urchins. Supported by Sea Grant and Saltonstall–Kennedy to CWW and MPL.

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Effect of Temperature, Water Flow, and Feed Formulation on Feeding, Respiration, and Production of *Strongylocentrotus droebachiensis* (Echinodermata: Echinoidea)

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Culture temperature, rate of water flow, and composition of prepared feed can affect processing of food and allocation of nutrients to body compartments of *Strongylocentrotus droebachiensis*. Small echinoids (3.5 ± 2 g wet weight and 19.1 ± 0.5 mm HD, means ± 1 SEM) were maintained for 16 wk during May through August in aquaria at 5 or 11°C in individual 530-ml containers with low or high rates of water flow (342 ± 20 or 921 ± 49 ml min^{-1}) and fed ad libitum on feeds manufactured from grains, soy, and fish meal. One feed also contained kelp meal. Individuals grew significantly ($P \leq 0.05$) in mass and horizontal diameter over the time course of feeding. Neither feeding rates nor absorption efficiency of organic material were significantly affected by water flow, temperature, or feed formulation. However, slightly more feces were produced by individuals at 11°C and by individuals consuming feed containing kelp, indicating that both temperature and food quality affect digestive processing. Oxygen consumption was not affected by temperature or feed formulation but did vary significantly with water flow. Higher respiration of individuals reared under low water flow, when placed in a circulating closed chamber respirometer, may reflect increased oxygen transport across the epithelium or an increase in activity when exposed to greater water flow within the respirometer. Temperature significantly affected whole animal growth, but water flow and feed formulation did not. Individuals grew 0.24 ± 0.03 g wk^{-1} at 11°C and 0.17 ± 0.02 g wk^{-1} at 5°C. Similarly, gonad indices were significantly higher in individuals reared at 11°C, while gut, lantern, and test indices were significantly higher in individuals reared at 5°C. Gut indices were significantly lower for individuals reared under low water flow than for individuals reared under high water flow. Culture conditions may affect digestive processing, metabolism, and production within body compartments of echinoids. Both feed formulation and culture conditions should be considered when fostering optimal production in echinoids.

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Gonad Production in the Sea Urchin *Lytechinus variegatus* (Lamarck) Fed Prepared Diets

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As management of the fisheries worldwide has not been successful, intensive efforts are being developed for aquaculture to meet the demand for sea urchins. The Gulf of Mexico does not have an established fishery for sea urchins, but one species shows great potential for a fishery and for aquaculture. *Lytechinus variegatus* exhibits rapid growth, and individuals reach gonadal maturity in less than 1 yr. We measured roe production in adults fed two prepared diets for a period of 10 wk in the laboratory. Gonads increased in size in individuals fed either diet, although roe production was less than the maximal roe production observed in natural populations. Gonad color varied with diet and was attributed to differences in the primary ingredients of each feed. Proximate composition of the gonads indicated that diet had no effect on carbohydrate (average 20.4% dry weight) and lipid (average 18% dry weight) levels; however, protein levels increased significantly with both diets (average 28.6% dry weight). Carbohydrate levels can vary by almost an order of magnitude (from 3 to 35% dry weight) and were, in part, dependent on the gonad index. This is particularly apparent in those individuals with GI values less than two. Thus, carbohydrate levels may reflect the nutritional well-being of the individual. Much of the carbohydrate is presumed to be glycogen (based on the presence of Na_2SO_4-precipitated, anthrone-reactive material). This research was supported by Mississippi–Alabama and Florida Sea Grants.

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Estradiol, Testosterone, and Progesterone Affect Ovarian Development in the Echinoid *Lytechinus variegatus*

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Environmental factors are known to influence reproduction of echinoids. These cues are transduced into endogenous signals that regulate gamete differentiation and growth of the mature gonad. In many organisms, control of these processes involves the sex steroids. The purpose of this study was to examine the influence of oral administration of estradiol (E), progesterone (P), and testosterone (T) on the ovaries of mature *Lytechinus variegatus* during gonadal growth. Echinoids were fed a formulated diet supplemented with steroids for 36 d. Only the mean ovary index (10.0 ± 1.1) from individuals fed E was significantly higher than the mean ovary index (6.5 ± 0.7) from individuals fed the control (C) diet ($P < 0.05$), suggesting that E may stimulate ovarian growth. E, P, EP, and P and finasteride (F, a 5α-reductase inhibitor) inhibited oocyte growth while T and TF promoted oocyte growth. Ovarian growth in individuals fed E was the result of proliferation of nutritive phagocytes and/or proliferation of oocytes, but not the result of oocyte growth. No significant differences in the levels of carbohydrate (mean = 23.5 ± 0.8% DW) or lipid (mean = 21.1 ± 0.5% DW) were determined among all treatments. Soluble proteins in individuals fed E (21.8 ± 1.0% DW, $P = 0.003$) and T (21.1 ± 0.8% DW, $P = 0.005$) were significantly higher than individuals fed C (17.3 ± 0.7% DW). Soluble proteins in individuals fed C were significantly higher than in individuals fed EP (11.8 ± 0.3% DW, $P = 0.001$), P (14.6 ± 0.3% DW, $P = 0.008$), PF (13.1 ± 0.7% DW, $P = 0.005$), or TF (9.4 ± 0.4% DW, $P = 0.001$). These data suggest that estrogens and 5α-reduced androgens may promote protein synthetic activity in the ovaries of echinoids; the types and amounts of proteins synthesized require further analysis.

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An Investigation into the Relationship Between Magnesium, Echinoderm Skeletal Proteins, and Calcium Carbonate

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Echinoderm skeletons, composed of magnesium-rich calcite are deposited intrasyncytially with the growing calcite surrounded by a layer of organic material within an intrasyncytial vacuole (Markel et

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al., 1986). Four characterized protein fractions extracted from the skeleton of the clypeasteroid *Mellita tenuis* were used in in vitro experiments to investigate their effects at different concentrations on calcium carbonate crystal formation. Experiments were conducted with substitution of varying quantities of calcium ions by magnesium ions to investigate protein–magnesium interactions and the resulting effects on crystallization. The effects of proteins upon calcium carbonate crystal nucleation and morphology were investigated using methods described by Albeck et al. (1993). To investigate any interaction between protein and magnesium ions, similar experiments were set up with the replacement of 10 and 50% of the calcium ions by magnesium. In all experiments, the total cation concentration was kept constant. Crystals were scored by number and shape using scanning electron microscopy. Seven different crystal morphologies were observed. The resulting data were analyzed nonparametrically to determine the effect of protein fractions and magnesium on crystal formation. The protein fractions in this experiment affected crystal numbers and formation, particularly in the presence of magnesium. It is suggested that the echinoderm macromolecules interact with magnesium and that this interaction is necessary to form a normal echinoderm skeleton.

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Ingestion, Absorption, and Gonad Production of Adult *Strongylocentrotus franciscanus* Fed Different Rations of a Prepared Diet

SUSAN C. MCBRIDE, J. M. LAWRENCE, AND A. L. LAWRENCE

Adult *Strongylocentrotus franciscanus* were fed two rations of an extruded diet for 62 d. Mean test diameter and whole weight of an initial sample was 91 ± 2 mm, 295 ± 18.4 g (mean ± SE, n = 16). The test rations used were 1 g dry feed/d or 3 g/d. An unfed control group was also maintained. Eight sea urchins per treatment showed significant differences in food ingestion rate, total organic absorption, gonad index, gut index, and moisture content of the gonad (all $P < 0.001$) but not in test diameter, whole animal weight, or gonad efficiency (all $P > 0.200$). Histological analysis of the gonads showed the *S. franciscanus* in the two ration treatments developed from the spent to the growing or premature stage while the unfed controls lost nutritive tissue or remained in the spent condition. Sea urchins consumed 42% more dry prepared diet in the higher ration and increased in gonad production at 1% or 0.4%/wk in the high and low rations, respectively.

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