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SCIENTIFIC STUDIES OF SEA URCHIN ECOLOGY: AN ANNOTATED BIBLIOGRAPHY

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BEHAVIOURAL ECOLOGY

1. Barnes, D.K.A. and A.C. Crook. 2001. Quantifying behavioural determinants of the coastal European sea-urchin *Paracentrotus lividus. Marine Biology* 138: 1205-1212.

This study, conducted at Lough Hyne, Ireland was aimed at investigating and quantifying the influence of interacting variables upon covering (placement of objects on upper surface) and migration (movement between upper and lower rock surfaces) behaviour by the sea urchin, *Paracentrotus lividus*, using loglinear analysis. The resultant model ranked the factors influential in covering behaviour as follows: (1) availability of covering items; (2) migratory behaviour; (3) size of *P. lividus*; (4) time of day; (5) time of year and (6) predatory intensity. However, the same variables were ranked differently for migratory behaviour. The model demonstrated, for the first time, an unequivocal relationship between covering and migration. Covering was most intense for upper-rock-surface individuals, during daylight periods and in summer supporting the theory that echinoids may cover to avoid over-exposure to light. The study also concluded that upper rock surfaces are important sources of food while lower surfaces provide refuge hence the migration. Models such as these provide baseline information on the relative importance and interrelationship of factors of complex behaviour.

2. Bernstein, B.B., B.E. Williams and K.H. Mann. 1981. The role of behavioural responses to predators in modifying urchins' (*Strongylocentrotus droebachiensis*) destructive grazing and seasonal foraging patterns. *Marine Biology* 63: 39-49.

   Spatial and temporal patterns of urchins (*Strongylocentrotus droebachiensis*) and periwinkles (*Littorina littorea*) have been investigated in three habitats: beds of *Laminaria longicruris* and *L. digitata*, an urchin dominated barren and the edge of a kelp bed forming a boundary between the two. Urchins were rare in the kelp beds and when large urchins did occur it was out of protection response from crabs and lobsters. Urchins were dominant in the barrens and in summer when the predaceous fish were active during day, they foraged at night. The urchins formed a dense feeding front along the kelp bed edge. The aggregating behaviour of urchins portrays an effective defense against some predators. These aggregations then graze destructively on *Laminaria spp.*, forming barrens that seem to be a new, stable configuration of the system.

3. Black, R., C.Codd, D. Herbert, S. Vink and J. Burt. 1984. The functional significance

of the relative size of Aristotle’s lantern in the sea urchin *Echinometra mathaei* (de Blainville). *Journal of Experimental Marine Biology and Ecology* 77: 81-97.

This paper points out the functional significance of the relative size of Aristotle’s lantern in *Echinometra mathaei*. An experimental study was undertaken where urchins were transplanted into same microhabitats and their gut material contents were weighed relative to the lantern sizes. The urchins with larger jaws had smaller relative weights of spines and gonads and removed larger areas of benthic algae compared with the smaller individuals. These observations justified that a possible trade-off existed in allocating the resources between relative size of the lantern and the gonad and spine sizes.

4. Black, R., M.S. Johnson and J.T. Trendall. 1982. Relative size of Aristotle’s lantern in *Echinometra mathaei* occurring at different densities. *Marine Biology* 71: 101-106.

   Relative lantern sizes to maximum test diameter were quoted for two consistent years 12 months apart for *Echinometra mathaei* at Rottnest Island, western Australia. The study showed that decreased food availability initiated relatively larger lanterns as a response to starvation period. Similar scenario was observed for urchin species in Zanzibar and Oregon (USA). However, further studies are required to confirm such an estimate of food availability.

5. Constable, A.J. 1993. The role of sutures in shrinking of the test in *Heliocidaris erythrogramma* (Echinoidea: Echinometridae). *Marine Biology* 117: 423-430.

   Sea urchin, *Heliocidaris erythrogramma,* were collected in January 1987 from Pt. Lillias in Corio Bay, Australia to examine the width of sutures and verify if a decrease in the width is the basis for test shrinkage of urchins during low food conditions. Data revealed less suture widths and lower gonad volumes in the low food treatment compared with the high food treatment after 4 months. Hence, urchins that undergo morphological change may be in a poor body condition to reproduce. A comparison of the observed and expected suture widths confirmed that decrease in suture width led to test shrinkage.

6. Edwards, P.B. and T.A. Ebert. 1991. Plastic responses to limited food availability and spine damage in the sea urchin *Strongylocentrotus purpuratus* (Stimpson). *Journal of Experimental Marine Biology and Ecology* 145: 205-220.

   A purple sea urchin, *Strongylocentrotus purpuratus*, demonstrated phenotypic variation in the intertidal zone in response to food limitation and wave action resulting in spine damage. Changes in overall size, test weight, and jaw length were monitored under laboratory conditions as urchins were subjected to varying food levels and spine damage. Food availability influenced overall growth to a greater extent than spine damage. Spine repair was found to stimulate overall calcification.

7. Grunbaum, H., G. Bergman, D.P. Abbott and J.C. Ogden. 1978. Intraspecific agonistic behaviour in the rock-boring sea urchin *Echinometra lucunter* (L.) (Echinodermata: Echinoidea). *Bulletin of Marine Science* 28, no.1: 181-188.

   Agonistic behaviour of *Echinometra lucunter* (L.) was studied on the algal ridges of Boiler Bay, St. Croix, U.S. Virgin Islands. Urchins created burrows on reef surfaces. Sixty-four set-ups were studied where urchins in burrows were classed hosts and the ones near the openings were intruders. Fourty six cases showed agonistic behaviour in form of pushing and biting which evicted most intruders. Occasionally, the host was evicted and sometimes both cohabited. This behaviour explains the dense *Echinometra* distribution in the wave-swept areas, which enhances niche establishment.

8. Ikuo, H., I.Yuko and T. Kazuya. 1999. Development of an experimental system to determine the diel behaviour of creeping animals, with special emphasis on gastropods and sea urchins. *Bulletin of the Japan Sea National Fisheries Research Institute* 0, no.49: 1-12.

   A high-tech informative recording system using time-lapse video through a very high sensitive ICCD television camera was developed and its effectiveness was tested and discussed while conducting behavioural experiments for creeping animals. Trial observations on the diel behaviours using the systems were conducted on the sublittoral topshell, *Omphalius rusticus* and the sea urchin *Strongylocentrotus nudus*. They demonstrated difference in diel activity and movement patterns. The system has provisions for recording experimental factors such as water temperature, dissolved oxygen and light intensity. The possibility of future usage is also discussed in this paper.

9. Levitan, D.R. 1991. Skeletal changes in the test and jaws of the sea urchin *Diadema antillarum* in response to food limitation. *Marine Biology* 111: 431-435.

   This was another study showing the plasticity that *Diadema antillarum* possesses of increasing the Aristotle's lantern size relative to test size. This investigation shows that its merely done by altering the ratio of test size and demipyramid. A proposal is put forward to study fossil specimens in attempt to investigate food availability in the recent and past times.

10. Mann, K.H., J.L.C. Wright, B.E. Welsford and E. Hatfield. 1984. Responses of the sea urchins *Strongylocentrotus droebachiensis* (O.F. Muller) to water-borne stimuli from potential predators and potential food algae. *Journal of Experimental Marine Biology and Ecology* 79: 233-244.

    The sea urchin *Strongylocentrotus droebachiensis* was introduced to water at 10-12 ^{0}C containing chemical attractants from predators such as lobsters and crabs. On 80% of the occasions, the urchin moved away. At lower temperature a higher proportion of the urchins were inactive but of the active ones, 80% moved away from the scent of predators. The same urchins moved towards water when it was passed over *Laminaria*, however at reduced temperature a lower proportion moved towards water. The attractant in *Laminaria* is an unstable, volatile hydrophobic compound with a lower molecular mass.

11. Neill, B.J. 1988. Experimental analysis of burrow defense in *Echinometra mathaei* (de Blainville) on Indo-West Pacific reef flat. *Journal of Experimental Marine Biology and Ecology*115: 127-136.

    The distinct burrow-defense responses displayed by the Indo-Pacific *Echinometra* support suggestions of two distinct species. The urchins from outer reef flat at Guam (Mariana Islands) were commonly seen to defend their burrows, except from large intruders, unlike the inner reef flat inhabitants. Transplanted urchins from the inner reef flat to the outer did not show burrow defense while the outer reef urchins showed unaltered defensive tenor in the inner reef ambient. Empty burrows in the inner reef-flat were recolonized five times faster than the outer region.

12. Otter, G.W. 1932. Rock-burrowing echinoids. *Biological Review of the Cambridge Philosophical Society* 7: 89-107.

    This author has basically reviewed the rock-burrowing habits of all possible echinoids and the kind of rock inhabited. He also relays that echinoids do not rely on this behaviour for existence like molluscs rather, burrows provide an entire protection against waves, predators and desiccation and the urchins will not bore unless natural cavities are absent.

13. Russell, M.P. 1998. Resource allocation plasticity in sea urchins: rapid, diet induced, phenotypic changes in the green sea urchin, *Strongylocentrotus droebachiensis* (Miller). *Journal of Experimental Biology and Ecology* 220: 1-14.

Gonads in sea urchins are a store of nutrient and perform reproductive functions. An experiment was conducted on Swans Island, Maine to test the hypothesis that *Strongylocentrotus droebachiensis* from an area of low food quality will rapidly increase gonadal tissue in response to a sudden increase of high quality food. A group of urchins were collected from a site lacking preferred algae and some dissected to record percentage body components. The remaining were categorized into 4 groups of equal size and number. These were allocated 4 feeding treatments: *Alaria esculenta*, *Laminaria digitata, L. longicruris and Ascophyllum nodosum*. Half of the urchins in each treatment were dissected after 3 weeks and then 6 weeks. Significant differences were observed for all treatments with *A. esculenta* producing the greatest increase in the gonad-wet weight in the sixth week. Other body components, body wall, Aristotle's lantern and gut did not demonstrate differences among treatments. Hence, this study in the framework of other related studies reveals that sea urchins show resource allocation and phenotypic plasticity in response to environmental variation.

14. Scheibling R.E. and J. Hamm. 1991. Interactions between sea urchins (*Strongylocentrotus droebachiensis*) and their predators in field and laboratory experiments. *Marine Biology* 110: 105-116.

Field and manipulative experiments on the sea *urchin Strongylocentrotus droebachiensis* was conducted at Eagle Head, Nova Scotia, Canada between 1984 and 1986. The cryptic and aggregation behaviour was studied in relation to refuge and predator availability. Flight responses by the urchins were observed in the presence of a predator. The small and large juveniles were more cryptic while the small and large adults aggregated at the tank sides forming defense clusters. Observational and experimental data suggests that predation at the late juvenile and early adult stages may influence population structure, distribution and abundance of *S. droebachiensis*.

15. Shulman, M.J. 1990. Aggression among sea urchins on Caribbean coral reefs. *Journal of Experimental Marine Biology and Ecology* 140: 197-207.

Inter- and intraspecific aggression were examined for five species of sea urchins, *Echinometra lucunter, E. viridis, Diadema antillarum, Lytechinus williamsi, and Eucidaris tribuloides*, in the San Blas Islands of Panama. This was performed by placing an intruder next to an undisturbed resident and behaviour of both individuals was recorded. *E. viridis* and *E. lucunter* recorded 46-79% of agonistic interactions (pushing and biting) between conspecifics and congeners. Residents usually showed aggression and intruders only replaced the residents once they were equal to or bigger. *D. antillarum* exhibited biting behaviour against both species of *Echinometra* in 23-24% of the trials. Rare interactions occurred between *L. williamsi* and *E. tribuloides*. *E. tribuloides* was observed pushing and biting occasionally and twice observed biting *Echinometra*. Hence, two kinds of interactions occur among Caribbean sea urchins, (1) interspecific and intraspecific aggression among *Echinometra* and (2) predatory/aggressive attacks against *Echinometra* by *D. antillarum*. The former may place dispersal limits on *Echinometra* in relation to food and shelter while the latter may result in restriction to crevices in response to protection from *D. antillarum.*

16. Tsuchiya, M. and M. Nishihira. 1985. Agonistic behaviour and its effect on the dispersion pattern in two types of the sea urchin, *Echinometra mathaei* (de Blainville). *Galaxea* 4: 37-48.

Two types of *Echinometra mathaei*, type A which are white-tipped and type B which have entirely brown or greenish-brown spines were studied for agonistic behaviour on the Okinawan reef flats, southern Japan. Type A, which were frequently seen in aggregations were more aggressive than type B which showed uniform distribution. Experiments of burrows where artificial intruders were introduced demonstrated that type A generally drove away type B and with like types placed in foreign burrows, type B disliked its own type more than type A. Usually bigger urchins drove away the smaller ones. Such dispersion patterns presumably is a function of their behavioural traits.

BIOLOGY

17. Dix, T.G. 1970. Biology of *Evechinus chloroticus* (Echinoidea: Echinometridae) from different locations. 1. General. *New Zealand Journal of Marine and Freshwater Research* 4, no.2: 91-116.

This paper discusses the general habits, morphological variation, food, associates and predators of the endemic New Zealand echinoid *Evechinus chloroticus* (Val.). *E. chloroticus* is principally a rocky bottom dweller but adults, juveniles and tiny individuals often occupy a variety of microhabitats. The urchin commonly occurs in shallow subtidal areas (<12m), however some intertidal populations occur, particularly towards the north. A superimposed pattern of population and intra-population clumping is typical and densities often exceed 50 adults/m^2. Variation is observed for spine length, thickness and sharpness and test thickness between populations. Variation in test thickness is related to nutrition while differences in spination could be attributed to wave exposure. Areas showing algal abundance has algivorous urchins while urchins predominantly browse material from substrate when algae is sparse. The rhabdocoele, *Synedesmis sp.* (in the gut), ciliates (in gut and gonad), clingfish *Dellichthys morelandi* and the isopod *Exosphaeroma sp.* are close associates of the urchin. Known predators include the cymatiid gastropods *Charonia capax* and *C. rubicunda*, the seastar *Coscinasterias calamaria*, the blue cod *Parapercichthys colias* and snapper *Chrysophrys auratus*.

18. Dix, T.G. 1970. Biology of *Evechinus chloroticus* (Echinoidea: Echinometridae) from different localities. 2. Movement. *New Zealand Journal of Marine Freshwater Research* 4, no.3: 267-277.

Tagging experiments of *Evechinus chloroticus* were conducted in Third Bay, Kaikoura. Sites were marked and recoveries of 57%, 26% and 17% were made after 3, 6 and 9 months. The tagged urchins were recovered at marked sites whereby maximum distance moved between sites was 4.8m. Mean gonad indices and amount of food in the gut of tagged and untagged urchins were compared. Untagged urchins showed higher gonad indices and amount of food than tagged individuals. Tagged urchins also demonstrated suppressed test growth. The fall in tagged recoveries was attributed to mortality.

CARBONATE BUDGET

19. Carreiro-Silva, M and T.R. McClanahan. 2001. Echinoid bioerosion and herbivory

on Kenyan coral reefs: the role of protection from fishing. *Journal of Experimental Marine Biology and Ecology* 262: 133-153.

Echinoid bioerosion and its effect on carbon cycle and reef development was investigated and quantified on reefs of different status in Kenya. These reefs were: (1) protected within Marine National Parks, which excluded all forms of fishing, (2) a reef within a Marine Park, which was protected for 8 years (newly protected) and (3) unprotected reefs which experienced heavy fishing and some coral collections. Sea urchins such as *Diadema setosum* (Leske), *D. savignyi* (Michelin), *Echinothrix diadema* (Linnaeus) and *Echinometra mathaei* (de Blainville) were compared for their bioerosion and herbivory processes through laboratory gut content analysis and gut evacuation experiments. The large bodied *E. diadema* exhibited the highest bioerosion and herbivory rates (5.5 ± 0.9 and 2.2 ± 0.3 g individual^{-1} day^{-1}). The rest followed suite respective to size. Highest sea urchin densities were recorded at unprotected reefs (6.2 ± 1.5 individual m^{-2}) hence the herbivory and bioerosion rates were high as well, (450 ± 77 g algae m^{-2} year^{-1} and 1180 ± 230 g $CaCO_3$ m^{-2} year^{-1}). The protected reefs recorded 20 times lower sea urchin bioerosion and herbivory rates due to the low sea urchin densities. The newly protected reef, with intermediate number of sea urchins displayed intermediate rates. These findings demonstrate the importance of fishing to echinoid activity and subsequent reef development.

20. Conand, C., P.Chabanet, P. Cuet and Y. Letourneur. 1997. The carbonate budget of a Fringing reef in La Reunion Island (Indian Ocean): Sea urchin and fish bioerosion and net calcification. *Proceedings of the Eighth International Coral Reef Symposium* 1: 953-958.

Bioerosion rates of sea urchins (*Echinometra mathaei*) and fish (*Scarus sordidus*) were investigated on 3 zones of La Saline reef, outer reef flat TR1, reef flat TR2 and back-reef zone TR3. The recorded values showed highest rates 8.3 kg $CaCO_3$ m^{-2} yr^{-1} for TR1 reflected by the high densities observed, TR2 = 2.9 kg and TR3 = 0.4 kg. Fish populations recorded lesser bioerosive impact (< 0.2 kg $CaCO_3$ m^{-2} yr^{-1}) at all the stations due to low abundance and size. Flow respirometry and the alkaline anomaly technique were used to assess net calcification in winter and summer on the three zones.

21. Downing, N. and C.R. El-Zahr. 1987. Gut evacuation and filling rates in the rock boring sea urchin, *Echinometra mathaei. Bulletin of Marine Science* 41, no.2: 579-584.

This article reviews two methods of assessing algal and calcium carbonate consumption by the rock-boring urchin, *Echinometra mathaei* on the reefs of Kuwait in the northwestern Arabian Gulf. Gut filling rates of starved urchins placed on coral rock gave 1.4 g $CaCO_3$ / urchin / day while the gut emptying rate of removed animals gave 0.9 $CaCO_3$ / urchin / day.

22. Hibino, K., R. van Woesik. 2000. Spatial differences and seasonal changes of net carbonate accumulation on some coral reefs of the Ryukyu Islands, Japan. *Journal of Experimental Marine Biology and Ecology* 252: 1-14.

Short-term spatial changes in accretion and erosion were detected on (experimental) carbonate blocks on three different reefs of Ryukyu Islands, Japan according to season, location, depth and substrate-type. Summer season showed higher accretion and coralline algal coverage than winter season. Windward reefs showed similar carbonate patterns compared with leeward reefs. Massive (Holocene) *Porites* demonstrated highest net erosion, followed by Pleistocene carbonate and (Holocene) *Acropora*. High populations of *Echinometra mathaei* (de Blainville) were observed on the reef adjacent to large human populations. Moreover, the overall net carbonate loss correlated well with densities of *E. mathaei* type A.

23. Hutchings, P.A. 1986. Biological destruction of coral reefs. *Coral Reefs* 4: 239-252.

This review presents a detailed account of different agents of biological destruction such as grazers, etchers and borers and their mechanisms of bioerosion. The impact bioerosion has on the reef morphology together with the reasons for varying bioerosion rates over space and time are outlined in some detail. Though the review concentrates on the present day reefs, some consideration is given to ancient reefs.

24. Hutchings, P.A., W.E. Kiene, R.B. Cunningham and C. Donnelly. 1992. Spatial and temporal patterns of non-colonial boring organisms (polychaetes, sipunculuns and bivalve molluscs) in *Porites* at Lizard Island, Great Barrier Reef. *Coral Reefs* 11: 23-31.

    Another investigation was conducted on Lizard Island in regards to the spatial and temporal patterns of colonization by non-colonial boring organisms to dead *Porites* substrate over 4 years. All the three environments, windward slope, reef flat and lagoonal patch reef showed varying rates of borer colonization; windward slope being most preferred and lagoonal patch reef the least. Most groups showed inter-year variations in colonization with spring/early summer dominating and variations were explained in the framework of life histories. This study together with that of Kiene (in preparation) help to explain that the borer colonization variations cause variations in bioerosion rates.

25. Kiene, W.E. 1985. Biological destruction of experimental coral substrates at Lizard Island (Great Barrier Reef, Australia). Destruction biologique des substrats coralliens experimentaux a Lizard Island (Grande Barrie're, Australie). *Proceedings of the Fifth International Coral Reef Congress,* Tahiti 5: 339-344.

    Boring and grazing are two major processes affecting the carbonate budget of coral reef ecosystems. Hence, the estimates of destruction rates are a good indicator of reef growth. Long-term monitoring of erosion rates was performed on Lizard Island, in the northern Great Barrier Reef, on three different environments, the reef slope, reef flat and the lagoon. Each of these environments displayed difference in mechanisms and rates of biological destruction. Grazing dominated the reef slope within the 2.5-3.5 years while least grazing occurred on the flats. In both of these environments, sipunculans and polychaetes were major borers. The composition of infaunal boring community demonstrated a series of succession that varied between environments. Average measured rates also varied with time. Reef slope substrates experienced erosion rates of 2.71 kg m^{-2} yr^{-1} exposed for 3.5 years while reef flat and lagoon recorded values of 0.41 kg m^{-2} yr^{-1} and 1.95 kg m^{-2} yr^{-1} respectively for 3 years.

26. Kiene, W.E. 1988. A model of bioerosion on the Great Barrier Reef. *Proceedings of The Sixth International Coral Reef Symposium,* Australia. 3: 449-454.

The recent investigations on the dead coral substrates of The Great Barrier Reef has shown variations in the bioerosion rates between reefs at different stages of growth at sea level. The varying distribution of parrotfishes within and between reefs helps to explain the variation. Up to 9.11 kg m^{-2} yr^{-1} of carbonate erosion has been recorded in the experiments. The subtidal environments on immature reefs have displayed higher grazing destruction while reduced grazing and high encrustation rates on mature reefs maintain dead coral substrates. The latter processes insight greater borer excavations. The interactions of these bioerosion and accretion processes will be important in the reconstruction of ancient reef ambience.

27. Kiene, W.E. and P.A. Hutchings. 1992. Long-term bioerosion of experimental coral substrates from Lizard Island, Great Barrier Reef. *Proceedings of the Seventh International Coral Reef Symposium,* Guam 1: 397-403.

    Experimental investigations using dead coral substrates on Lizard Island have been occurring since 1980. This paper elucidates the bioerosion rates from 7 and 9 years. Similitude trends to previous studies were observed. Grazing dominated the subtidal region when compared with the flats and boring played a minor role in bio-destruction. The distribution of boring sponges, molluscs and worms was highly variable in space and time. Fluctuations in grazing and boring rates are seen to aid in reforming reefal environments.

28. Le Campion-Alsumard, T., J.C. Romano, M. Peyrot-Clausade, J. Le Campion and R. R. Paul. 1993. Influence of some coral reef communities on the calcium carbonate budget of Tiahura reef (Moorea, French Polynesia). *Marine Biology* 115: 685-693.

    This article aims to highlight the interaction of processes such as calcification and biological degradation, which are reflected in the chemical properties of the seawater overlying the reefs. This fact was proven through a series of experiments done on Moorea Island (French

Polynesia) in 1988 where the chemical properties of sea water was monitored diurnally and nocturnally in the field and under laboratory conditions. The results revealed that in the study area (Tiahura barrier reef flat), the calcium carbonate budget fluctuated as a function of location in the water current.

29. Pichon, M. 1985. Organic production and calcification in some coral reefs of Polynesia. *Proceedings of the Fifth International Coral Reef Congress,* Tahiti 6: 173-177.

Studies on organic production and calcification rates were conducted and compared for the different reef types around an elevated island (Moorea) in the Society Archipelago and one of the atolls off north west Tuamotu (Rangiroa). While the fringing reefs showed high organic production with lower calcification rates, the crustose coralline dominated-reefs of Rangiroa revealed slightly lower organic production with a comparative higher calcification rate.

30. Russo, A.R. 1980. Bioerosion by two rock boring echinoids (*Echinometra mathaei* and *Echinostrephus aciculatus* on Enewetak Atoll, Marshall Islands. *Journal of Marine Research* 38, no.1: 99-110.

This author used the turnover of gut content method to assess the bioerosion rates of *Echinometra mathaei* and *Echinostrephus aciculatus* on Enewetak Atoll. Both species collectively show a range of total $CaCO_3$

erosion of 80-325 g m^{-2} yr^{-1} while the estimated total annual production of $CaCO_3$ by the reef is 4000 g m^{-2} yr^{-1}. Hence, they can contribute from 2-8% of the total bioerosion on the atoll. *Cliona*, a sponge, is also a major bioeroder and can destroy up to 25% of the annual production.

COMMUNITY ECOLOGY

31. Anders, W., D.R. Norris and J. Templado. 1994. Descriptions of four new eulimid gastropods parasitic on irregular sea urchins. *The Veliger* 37, no.2: 141-154.

This paper basically reviews all the parasites of irregular sea urchins. It notes *Hypermastus mareticola* from Guam and *H. orstomi* from New Caledonia both parasitizing on the heart urchin, *Maretia planulata*. *H. obliquistomum* on the sand dollar, *Laganum depressum*; *Eulima encopicola* from the Galapagos parasitizes the sand dollar *Encope micropora galapagenis*; *Balcis clypeastericola* parasitizes clypeasteroid sea urchin *Clypeaster japonicus*; *C. natalensis* lives on *C. eurychoreus*. Also, two more notes of new species of Clypeastericola are recorded from *C. australasiae* and from *L. depressum* but they are left undescribed.

32. Andrew, N.L. 1988. Ecological aspects of the common sea urchin, *Evechinus chloroticus,* in northern New Zealand: a review. *New Zealand Journal of Marine and Freshwater Research* 22: 415-426.

Evechinus chloroticus (Val.) is a primary determinant of community structure on shallow subtidal rocky reefs in northern New Zealand. An inverse relationship exists between large brown algae and the sea urchin due to its grazing patterns. The availability of different brown algae and its preferences determines the urchins' diet. The grazing of these sea urchins also has an indirect effect on the molluscan herbivores and many fish species. Forces and processes acting to limit the actions of *E. chloroticus* are discussed. It was identified that rock lobsters and predatory fishes most likely affect the urchin abundance. However, these predators are not intense enough to control the effect of *Evechinus* on community structure.

33. Andrew, N.L. and J.H. Choat. 1982. The influence of predation and conspecific adults on the abundance of juvenile *Evechinus chloroticus* (Echinoidea: Echinometridae). *Oecologia* 54: 80-87.

Shallow, subtidal areas around northeastern New Zealand demonstrate reefs dominated by red algae and high densities of *Evechinus chloroticus*. Factors affecting the abundance of juvenile *E. chloroticus* were investigated. An experiment using factorial design was applied to assess the effect of predators and adult *E. chloroticus* on the juvenile abundance. Gut content analysis of predatory fish in the area revealed preying on the juvenile. Exclusion cages containing juvenile urchins demonstrated flourishing populations after 16 months. Removal of adult urchins resulted in rapid colonization by *Laminaria* and fucoid algae, predominantly

Ecklonia radiata and *Sargassum sinclairii*. Lower densities of herbivorous gastropods and predatory fish were observed in the experimental arena. Nature sees less but a consistent number of juvenile *E. chloroticus* escaping predation and contributing to the population structure. Hence, predators play a key role in structuring shallow water reef communities.

34. Bak, R.P.M. and G.Van Eys. 1975. Predation of the sea urchin *Diadema antillarum* Philippi on living coral. *Oecologia* 20: 111-115.

The sea urchin, *Diadema antillarum*, were observed as major predators of living corals on reefs of Curacao and Bonaire (Netherlands Antilles). They occurred in densities of 8.5 animals/m^2 and up to 8.2% of the population were feeding on coral surfaces at night. *Acropora* were the readily attacked species.

35. Carpenter, R.C. 1984. Predator and population density control of homing behaviour in the Caribbean echinoid *Diadema antillarum. Marine Biology* 82: 101-108.

The homing frequency (percent returns to the same crevice) of *Diadema. antillarum* was recorded to range from 30-84% among areas. Sites with higher predator-protected quality recorded higher homing percentage and vice-versa. Previously foraged areas are not visited until later. This predator-mediated behaviour pattern and its effects on coral reef communities suggests a natural ‘understanding’ between predator-sea urchin-algal relationships in temperate marine communities.

36. Chapman, A.R.O. 1981. Stability of sea urchin dominated barren grounds following destructive grazing of kelp in St. Margaret’s Bay, Eastern Canada. *Marine Biology* 62: 307-311.

St. Margaret’s Bay, Nova Scotia, in Canada was devoid of macroalgae for several years. The regeneration was destroyed within 10 months by sea urchins. An experiment where kelp regeneration was induced met a similar fate. The re-establishment of kelp population seemed unlikely even with the lowest sea urchin biomass and density. The sea urchin population required to suppress kelp regeneration is fed by benthic microalgae. Diatoms and other pioneer algal communities were observed in sea urchin guts. The mean standing crop of benthic microalgae was estimated to be 2.2 g C m^{-2} and the production as ca 15 g C m^{-2} yr^{-1} at 8m depth. The loss of primary production on the Bay has been attributed to destruction of kelp.

37. Dart, J.K.G. 1972. Echinoids, algal lawn and coral recolonization. *Nature* 239: 50-51.

This article suggests that the rich colonization of sea urchins observed on the reef crests of Sudanese Red Sea could be a function of high recruitment capabilities (successful settlement, metamorphosis and early growth) for coral planulae on grazed rock surfaces. Further, the algal distributions are discussed on various reefs relative to urchin densities.

38. Hendler, G. 1977. The differential effects of seasonal stress and predation on the stability of reef-flat echinoid populations. *Proceedings of Third International Coral Reef Symposium* 1: 217-223.

Nine species of echinoids were studied for their mortality patterns over 58 weeks on a fringing reef flat at Galeta, Panama. The principal cause of mortality was physical stress that occurs twice yearly, generated by extended subaerial exposures of the reef platform. Other factors included shorebirds and predatory gastropod, *Cypraecassis testiculus*. Urchin species from the more exposed areas experienced frequent death and reached sexual maturity in less than a year compared to the cryptic populations which showed more resistance to stress and reproduced in the second year of growth. However, the latter types appeared more vulnerable to predation than the former but the loss due to predation was more trivial than physical stress. The answer to discrepancies lies in trade-off between the effects of stress and predation intensity.

39. Hughes, R.N. and H.P.I. Hughes. 1971. A study of the gastropod *Cassis tuberosa* (L.) preying upon sea urchins. *Journal of Experimental Marine Biology and Ecology* 7: 305-314.

This paper aimed to outline the mechanism by which *Cassis tuberosa* (L.) feeds on different species of sea urchins. It detects its prey via chemoreception and generally bores a hole into the urchin with its radula to suck out everything but the gut of the urchin. Afterwards tube feet and the spines are consumed in varying proportions. *C. tuberosa* demonstrated preference for *Echinometra lucunter* (L.) when presented with equal numbers of similarly sized sea urchins. *Tripneustes ventricosus* (Lamarck) was the second most preferred. *Diadema antillarum* (Phillipi), *Eucidaris tribuloides* (Lamarck), *Meoma ventricosus* (Lamarck) and *Mellita quinquiesperforata* (Leske) were not eaten. Changes in the number of prey eaten against the number of prey offered was plotted to obtain a type 2 functional response curve for *C. tuberosa* feeding on *E. lucunter*.

40. Keller, B.D. 1983. Coexistence of sea urchins in seagrass meadows: an experimental analysis of competition and predation. *Ecology* 64, no.6: 1581-1598.

An experimental examination was undertaken at two sites, of competition and predation on *Tripneustes ventricosus* and *Lytechinus variegatus,* the common sea urchins in meadows of *Thalassia testudinum*. The study concluded that intraspecific competition and predation on recruits influence their population dynamics. Briefly, *Tripneustes* grazing influenced *Thalassia* biomass while the urchins mortality was not significantly affected by *Lytechinus*, and recruitment of *Tripneustes* was sparse at one site and did not increase when predators were excluded and was inversely related to the density of adults. *Lytechinus*, on the other hand, had a more generalized diet, had a moderate effect on *Thalassia* and substantially declined at densities 16 times greater than its naturally occurring abundance. Recruitment of *Lytechinus* decreased as *Tripneustes* density increased, but remained unaltered when predators were excluded. *Tripneustes* showed a higher growth rate than *Lytechinus*. Coexistence of these urchins seems to be mediated by difference in diet hence resulting in insignificant interspecific competitive effects on mortality, growth and fecundity.

41. McClanahan, T.R. 1988. Coexistence in a sea urchin guild and its implications to coral reef diversity and degradation. *Oecologia* 77: 210-218.

This article relays the reasons for coexistence between the coral reef inhabiting sea urchins, *Echinometra mathaei*, *Diadema savignyi and D. setosum*. This was done via comparison of body morphology, distribution, diet, susceptibility to predators, intra- and interspecific competition and settlement rates. The three species share similar diets and habitats except for some microspatial preferences. *E. mathaei* has high settlement rates, is the smallest and lives territorially within crevices or burrows. *D. savignyi*, intermediate in size, lives frequently in intermediate size burrows or social groups. *D. setosum*, the largest species, lives in large crevices or occasionally in social groups. *E. mathaei* was consistently the top competitor for space while *D. savignyi* won between the *Diadema* species.

Coexistence was noted to be a function of predation on the competitive-dominant while predation coupled with different body morphology and behaviour allowed spatial resource partitioning of the reef's variable topography.

42. McClanahan, T.R. 1992. Resource utilization, competition, and predation: a model and example from coral reef grazers. *Ecological Modelling* 61: 195-215.

A simple biomass-based energetic model was developed to help explain the energetic requirements of organisms for resource competitive ability and the consequent trade-off that herbivores need to adjust to sustain themselves under predation. Sea urchins out compete herbivorous fish due to lower respiration and consumption rates when their predators are reduced (overfishing) and reach maximum biomass levels an order of magnitude higher than the fish. Simulations of a hypothetical herbivore indicate that herbivore steady-state biomass increases with decreasing consumption rates. Simulations of competition between hypothetical herbivores indicate that only the level to which a herbivore exhausts its resources is important in determining the top resource competitor, although biomass dynamics differ depending on feeding, gross production rates, and initial status of competitors. Hence, the model suggests that energetic trade-off in an organism's life history enables resource competition and tolerance to predation and disturbance.

43. McClanahan, T.R. 1995. Fish predators and scavengers of the sea urchin *Echinometra mathaei* in Kenyan coral-reef marine parks. *Environmental Biology of Fishes* 43: 187-193.

Observations were made on a variety of sites (0.5-3m deep) in 3 Kenyan marine parks during daylight and predators on 120 adult *Echinometra mathaei* were recorded. The predators (8 species) in decreasing order of abundance were triggerfish *Balistapus undulatus* (65%), terminal-male wrasses *Coris formosa*, *C. aygula* and *Cheilinus trilobatus* and the scavenger *Lethrinus mahsena*. The predators who readily failed were more numerous (11 species) and the scavengers of opened carcasses were the most speciose (20 species). These observations suggest the importance that fishery regulations can play in controlling urchin boom hence their detrimental consequences such as bioerosion and competitive exclusion of fishes.

44. McClanahan, T.R. 1998. Predation and the distribution and abundance of tropical sea urchin populations *Journal of Experimental Marine Biology and Ecology* 221: 231-255.

An intensive investigation of abundance, distribution and diversity of 9 species of sea urchins was performed in 7 reef lagoons of the Indian Ocean over 7 years. The population controlling factors that causes variation in time and space and the role predation plays in their ecology were determined. The amount of refuge was used to predict the abundance of individual species of sea urchin, species richness and diversity. Statistical manipulations aided in interpreting how diversity and number of species were strongly associated with measures of refuge and exhibited unimodal curves. Refuge resources got partitioned among species particularly for *Echinometra mathaei, Tripneustes gratilla* and *Diadema setosum* at the low to intermediate levels of predation. An overlap occurred in the peak abundance of *D. savignyi, Echinothrix diadema, Toxopneustes pileolus* and *Stomopneustes variolaris* at the highest levels of predation. However, the partitioning strategy is more evident at a smaller scale of reef crevices (< $10m^2$).

45. McClanahan, T.R. 1999. Predation and the control of the sea urchin *Echinometra viridis* and fleshy algae in the patch reefs of Glovers Reef, Belize. *Ecosystems* 2: 511-523.

After the mass mortality of *Diadema antillarum* in the mid-1980's, *Echinometra viridis*, a grazer sympatric with *D. antillarum*, has been studied extensively. More specifically, a closer look was taken at the role finfish and invertebrate predators play in controlling its distribution and how this urchin controls the exposed fleshy algae on the patch reefs of the Glovers Reef Atoll lagoon. Major predators included *Calamus bajonado* (jolthead porgy), *Balistes vetula* and *Canthidermis sufflamen* (queen and ocean triggerfish), *Lachnolaimus maximus* (hogfish), and a gastropod. These predators restrict *E. viridis* to cryptic locations. A positive correlation was observed between *E. viridis* and fleshy algae abundance but a negative one with the frequency of finfish bites. Sea urchins grazed algal assays less than the finfish. Due to a close association between net benthic primary production and herbivory on exposed surfaces, *E. viridis* appears to be less effective in maintaining the same production as *D. antillarum*.

46. McClanahan, T.R. and N.A. Muthiga. 1989. Patterns of predation on a sea urchin, *Echinometra mathaei* (de Blainville), on Kenyan coral reefs. *Journal of Experimental Marine Biology and Ecology* 126: 77-94.

Four Kenyan coral reefs, two fished and two protected were investigated for factors affecting predation rates of *Echinometra mathaei*.

Three hypotheses were tested (1) predation should be lower on fished reefs compared to unfished reefs, (2) predation should be lower in shallower waters and therefore between reefs as a function of water depth and (3) predation should be lower with increasing sea urchin body size. The key predation factor was attributed to finfish 90%, asteroids 5% and gastropods 5%. The depth factor was more important in protected reefs. Hence, within fished reefs, a reduction in predator leads to increase in sea urchin density and expansion of distribution range to deeper areas. Consequently, we expect higher bioerosion rates at greater depths on heavily fished reefs.

47. McClanahan, T.R., M. Nugues and S. Mwachireya. 1994. Fish and sea urchin herbivory and competition in Kenyan coral reef lagoons: the role of reef management. *Journal of Experimental Marine Biology and Ecology* 184: 237-254.

Two protected reefs for over 15 years, one transition reef protected for ~ 2 years and three unprotected reefs were studied for the impact of overfishing by *Thalassia* and *Sargassum* bioassays. More specifically, the study focussed to (1) assess the ability of a herbivory assay to distinguish between herbivore types (a) sea urchins and (b) herbivorous fishes (parrotfish and surgeonfish), (2) observe potential impacts of coral reef herbivores on seagrass species composition and abundance, and (3) display the role fishing plays in mediating competitive interactions between the herbivore types. Parrotfishes dominated assay herbivory while *Echinothrix diadema* exhibited much higher preference from other species. Between-site comparison had limitations. Variation existed between species composition of herbivore type and their feeding preferences.

48. Parker, D.A. and M.J. Shulman. 1986. Avoiding predation: alarm responses of Caribbean sea urchins to simulated predation on conspecific and heterospecific sea urchins. *Marine Biology* 93: 201-208.

Sea urchins, *Echinometra viridis, E. lucunter, Lytechinus variegatus, L.williamsi*, *Tripneustes ventricosus*, *Diadema antillarum and Eucidaris tribuloides* were collected along the Caribbean coast during October 1984 and December 1985 to investigate their alarm responses to the extracts of conspecifics and heterospecifics. Responses to seawater and extracts of gnathostomate echinoid *Clypeaster subdepressus* were used for controls. Alarm response intensities were measured by: (1) the percentage of individuals that responded by moving away from the extract and/or towards shelter and (2) the mean distance moved. Species which lived in sheltered microhabitat conditions such as *Diadema antillarum* and *Lytechinus variegatus*, moved away from the direction of the extracts. *Echinometra viridis*, *E. lucunter* and *L. williamsii* responded to sea urchin extracts by moving towards shelter sites. The distance that individuals of each species moved initially following exposure to conspecific extracts was correlated with the distance that species moved from shelter while foraging. *Eucidaris tribuloides* did not exhibit alarm response to either extract as it naturally secures itself with stout spines in protected sites within corals. Similarly, *D. antillarum* that inhabited long, dense seagrass showed no alarm responses. *T. ventricosus* showed a weak response to extracts of *L. variegatus* but no response to extracts of other species, the reasons to which is unclear. For the species that demonstrated an alarm response to sea urchin extracts, the intensity varied depending on the type of extract used. *L. variegatus*, *L. williamsii* and *D. antillarum* responded strongly to extracts form conspecifics while *Echinometra viridis* and *E. lucunter* responded strongly to extracts from both conspecifics and congeners. The weakest responses were seen for *T. ventricosus* and *E. tribuloides*. Patterns of alarm responses to the extracts of heterospecific sea urchins could not be consistently explained by overlap in habitat and predators and phylogenetic relationships.

FEEDING ECOLOGY

49. Amsler, C.D., J.B. McClintock and B.J. Baker. 1999. An Antarctic feeding triangle: Defensive interactions between macroalgae, sea urchins and sea anemones. *Marine Ecology Progress Series* 183: 105-114.

This article reviews the trio relationship that exists between macroalgae (*Phyllophora antarctica* and *Iridaea cordata*), the sea urchin *Sterechinus neumayeri*, and the sea anemone *Isotealia antarctica* in Antarctica. The urchin makes good use of the algae as a refuge and defense against *I.antarctica*. This defense is physical, as thalli from which defensive chemicals have been extracted are equally protective. Macroalgae benefits as it gets to contribute to the gene pool of the fertile drift plants in the photic zone. The urchins also enhance the distribution of the macroalgae.

50. Ayling, A.L.1978. The relation of food availability and food preferences to the field diet of an echinoid *Evechinus chloroticus* (Valenciennes). *Journal of Experimental Marine Biology and Ecology* 33: 223-235.

The increasingly disturbing foraging behaviour of echinoids was investigated in the marine communities. The field diet of *Evechinus chloroticus* was investigated in relation to food availability and food preferences. *E. chloroticus* is a generalist grazer and this study was done on populations grazing encrusting communities dominated by sponges. The field results showed urchins grazing sponges according to abundance. However, in the laboratory, food preferences were observed for two populations of *E. chloroticus* when presented with 24 species of sponges. One population was picked from an intertidal reef, which rarely had sponge communities and the other from a sublittoral habitat where sponges were dominant. The sponge used as food also came from two different areas: one where urchins were almost absent and the other where urchins were abundant and were seen feeding on sponges. When presented with unfamiliar species of sponges, urchins from both groups ranked sponge species similarly. The food preferences did not relate to the field diet of the urchins. This paper discusses the reasons for difference between experimental results and field observations.

51. Barker, M.F., J.A. Keogh, J.M. Lawrence and A.L. Lawrence. 1998. Feeding rate, absorption efficiencies, growth and enhancement of gonad production in the New Zealand sea urchin *Evechinus chloroticus* Valenciennes (Echinoidea: Echinometridae) fed prepared and natural diets. *Journal of Shellfish Research* 17, no.5: 1583-1590.

Three size classes of sea urchins, *Evechinus chloroticus*, small (30-40mm), medium (50-60mm) and large (70-80mm) were collected from Doubtful Sound on the west coast of the South Island of new Zealand and kept in individual containers with running seawater. The urchins were fed prepared and natural feed and assessed for feeding rates, absorption efficiencies, growth and gonad and gut indices at the beginning and end of every experimental period. The experiment was monitored seasonally. Feeding rates differed significantly between diets whereby urchins ate more extruded pellets than agar-bound prepared feed or natural algae. Feeding rate also showed a seasonal trend correlated with water temperature. Absorption was quite variable and was the least in December. Gonad indices were higher when fed prepared feeds, however seasonal differences prevailed. Small urchins matured quickly and produced white- or cream-coloured gonads compared to immature ones in the wild. Also, the wild urchins produced yellow/orange gonads. Gut indices were similar in all the size classes and were generally higher for urchins fed prepared meals. Smaller urchins grew more in proportion than the other two size classes.

52. Carpenter, R.C. 1981.Grazing by *Diadema antillarum* (Philippi) and its effects on the benthic algal community. *Journal of Marine Research* 39, no.4: 749-765.

Experimental studies conducted in St. Croix, U.S. Virgin Islands and Discovery Bay, Jamaica reveal similar results that *Diadema antillarum* has

a strong feeding preference for algal turf but a seasonal reduction in this switches its preference to live coral predation. Enclosure experiments show that intermediate urchin densities result in maximization of algal species richness. Collations from all studies show that a strong inverse relationship exists between urchin density and mean individual urchin size and urchin density and algal abundance both naturally and in controls.

53. Cole, R.G. and T. Haggitt. (In press). Dietary preferences of *Evechinus chloroticus*. *Proceedings of 10th International Echinoderm Conference*.

The dietary preferences of *Evechinus chloroticus* was examined using both lab and field experiments, to examine the persistence of fucalean *Carpophyllum flexuosum* on "barren" areas in northeastern New Zealand. *Evechinus* has the ability to distinguish between seaweeds in the field. *C. flexuosum*, which is the least palatable, is the less preferred both in field choice assays and lab choice experiments. Exhaustive densities *of E. chloroticus* resulted in destructive grazing of dominant laminarian, *Ecklonia radiata* while *C. flexuosum* suffered little mortality. The phlorotannin levels in laminae of *C. flexuosum* ranged from about 12% to over 25% and it is believed that it is the dietary preference *of E. chloroticus* that results in the persistence of *C. flexuosum*.

54. Duggins, D.O. 1981. Sea urchins and kelp: The effects of short-term changes in urchin diet. *Limnological Oceanography* 26, no.2: 391-394.

Sea urchins tend to structure the benthic algal associations in shallow subtidal communities by their feeding patterns. An interruption in their feeding mode from algae to benthic diatoms and pelagic salps resulted in an increase in kelp abundance in 1978 in Torch Bay, Alaska.

55. Greenway, M. 1995. Trophic relationships of macrofauna within a Jamaican seagrass meadow and the role of the echinoid *Lytechinus variegatus* (Lamarck). *Bulletin of Marine Science* 56, no.3: 719-736.

Feeding methods of macrobenthic invertebrates and fish fauna were sampled in the seagrass meadow of *Thalassia testudinum* in Kingston Harbour, Jamaica. Gastropods were found to be dominant epiphyte grazers while echinoid, *Lytechinus variegatus* was a major consumer of seagrass blades. Crustaceans were the most diverse group of detritivores though nemerteans, sipunculids and ophiuroids were numerically dominant. Bivalves dominated suspension feeding and omnivorous species included nereid polychaetes and a variety of decapod crustaceans. Diet preferences of fish species were deduced.

56. Hart, L.J. and F.S. Chia. 1990. Effect of food supply and body size on the foraging behaviour of the burrowing sea urchin *Echinometra mathaei* (de Blainville). *Journal of Experimental Marine Biology and Ecology* 135: 99-108.

Foraging behaviour of *Echinometra mathaei* was monitored under laboratory conditions. The population was divided into three size classes and exposed to two treatments; in one the animals were fed daily and in the other they were starved for 34 days. Fed animals remained sedentary while the starved ones increased foraging frequency. The intermediate-sized were most inclined to forage for food. Size-related differences in foraging could well be explained by differing food requirements, susceptibility to predation and intraspecific competition for space.

57. Hay, M.E. 1984. Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? *Ecology* 65, no.2: 446-454.

Thalassia testudinum field bioassay was used on 11 coral reefs scattered throughout the Caribbean to assess herbivory rates of urchins and fish relative to the fishing pressure and depth factor. Overfished reefs showed high urchin densities with grazing equal to or higher than fish grazing and high *Thalassia* strip removal with depth. Reefs subject to little pressure revealed high urchin densities with all strips being removed by fish with the rate decreasing with depth. It is doubtful that all the interactions observed is unaffected by humans.

58. Hay, M.E., T. Colburn and D. Downing. 1983. Spatial and temporal patterns in herbivory on a Caribbean fringing reef: the effects on plant distribution. *Oecologia* 58: 299-308.

Field bioassay of *Thalassia testudinum* blades was used to assess the impact of herbivorous fishes and urchins in different habitats, at variable depths and at differing times of the day on a fringing reef at Galeta Point, Panama. Additional algal transplants helped deduce the effect of herbivory on algal distribution and on potential plant-plant interactions in the absence of grazers. Herbivorous fishes dominantly fed diurnally and removed more than 90% of the *Thalassia* while the urchins didn't show any preference for feeding time and only accounted for 9% removal. Algal species from the reef flat and sand plain were excluded from the reef slope by herbivores and would out compete reef slope species in the absence of herbivory.

59. Klinger, T.S. and J.M. Lawrence. 1985. Distance perception of food and the effect of food quantity on feeding behaviour of *Lytechinus variegatus* (Lamarck) (Echinodermata: Echinoidea). *Marine Behavioural Physiology* 11: 327-344.

The food search strategy of *Lytechinus variegatus* was investigated using extracts of *Thalassia testudinum* and *Gracilaria verrucosa*. The experiment showed that unlike many carnivorous marine invertebrates, *L. variegatus* depends more on random encounters than upon directed movement as a search strategy. This indicated the strong difference between carnivore and herbivore feeding strategies. The frequency of feeding had no effect upon the feeding rate of large urchins. Small urchins consumed less food when fed at intervals as an effect of starvation. This suggested that *L. variegatus* has a constant rate of ingestion, independent of hunger or of satiation, within the constraints of their well being. However, individuals fed *ad libitum* moved faster than the starved ones suggesting scarce food demands reduced energy expenditure and that movement is increased to exploit available resources when food is abundant.

60. Larson, B.R., R.L. Vadas and M. Keser. 1980. Feeding and nutritional ecology of the sea urchin *Strongylocentrotus drobachiensis* in Maine, USA. *Marine Biology* 59: 49-62.

An experimental study done on the food preferences of *Strongylocentrotus drobachiensis*, a sea urchin, exhibited the feeding strategy that the urchin has evolved which maximizes its growth and reproduction. The article gives a list of preferred food, *Laminaria longicruris*, *Chondrus crispus*, *Corallina officinalis*, *Ascophyllum nodosum* and *Agarum cribrosum* and how they switch preferences seasonally. The study also revealed that though caloric intake positively correlated with preference, it’s only because of high feeding rates of preferred food. Urchin feeding performance was also monitored as they were switched from preferred to non-preferred food.

61. Lawrence, J.M. 1975. On the relationships between marine plants and sea urchins.

Oceanographic Marine Biology Annual Review 13: 213-286.

This review gives an account of the sea urchins as dominant marine herbivores and the impact their feeding has on the abundance and distribution of marine plants in shallow water marine environments. It also elaborates on the biology of feeding and utilization of food.

62. Lewis, J.B. 1964. Feeding and digestion in the tropical sea urchin *Diadema antillarum* Philippi. *Canadian Journal of Zoology* 42: 549-557.

Diadema antillarum was investigated to principally feed on algae during the afternoon and early evening. This article basically describes *Diadema*'s feeding activities and the histology of its digestive tract.

63. Macia, S. 2000. The effects of sea urchin grazing and drift algal blooms on a subtropical seagrass bed community. *Journal of Experimental Marine Biology and Ecology* 246, no.1: 53-67.

Caging experiments were conducted at Biscayne Bay, Florida, to investigate the effects sea urchin grazing and drift algal blooms were having on floral and faunal components of the *Thalassia testudinum* beds. Abundance of sea urchins, *Lytechinus vareigatus*, and drift algae were manipulated within the cages. Winter recorded a decrease in seagrass shoot density and aboveground biomass. Similar effects were not evident in summer reflecting seasonal impact. Shoot density appeared more vulnerable to grazing than aboveground biomass maybe due to higher productivity of partly eaten leaves. Winter allows large algal mats to cover the seagrass canopy, which do not have significant negative effects under normal grazing regime. However, with increased grazing pressure, there is a synergistic effect of herbivory and drift algae on seagrass shoot density. At intermediate urchin densities (10 per m^{-2}), similar effect was witnessed. Invertebrate abundance at the field site was low compared with other seagrass beds.

64. Mattison, J.E., J.D. Trent, A.L. Shanks, T.B. Akin and J.S. Pearse. 1977. Movement and feeding activity of red sea urchins (*Strongylocentrotus franciscanus*) adjacent to a kelp forest. *Marine Biology* 39: 25-30.

Study was conducted on the movement and feeding activity of red sea urchins, *Strongylocentrotus franciscanus* inside a kelp forest and the seaward end of the forest. Urchin movement varied from 7.5cm/day inside to 50cm/day at 15 and 100m outside the kelp forest. The feeding activity decreased from 66% inside to 16 and 15% at 15 and 100m towards the seaward end. The data demonstrates that sea urchin movement increases to cater for food scarcity.

65. Morrison, D. 1988. Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. *Ecology* 69, no.5: 1367-1382.

This article compares the herbivory performance of sea urchins and fish on algae both in the shallow (<10m) and deep (>15m) coral forereef communities off Discovery Bay, Jamaica. The distribution and abundance patterns of the algal types (macroalgae, crustose coralline) were investigated and correlated with a decline in herbivory over depth. Algal transplants and grazer exclusion methods were used to test the hypothesis that herbivory affects algal abundance and distribution and details of the tests are discussed. The findings demonstrated that herbivory was largely responsible for the algal distribution. *Diadema* was found to contribute greatly to the shallow community but only a minor role relative to fishes in structuring the deeper community. Also, different herbivores were concluded to have a differential effect on the erect macroalgal composition.

66. Paine, R.T. and R.L. Vadas.1969. The effects of grazing by sea urchins, *Strongylocentrotus spp*., on benthic algal populations. *Limnological Oceanography* 14: 710-719.

Strongylocentrotus purpuratus were removed from the intertidal pools of Mukkaw Bay, Washington and *S. fransiscanus* from Friday Harbour to observe the rate and pattern of algal succession for periods up to three years. At first, new species were observed but later a single perennial brown algal species, *Hedophyllum sessile* in the intertidal and *Laminaria complanata* or *L. groenlandica*, dominated subtidally. The rate of dominance correlated with the area’s tidal height with rapid succession in the lower intertidal areas or subtidally. These plants did not exist in the

experimental sites before the urchin removal hence urchin browsing could make a principal contribution to the variety of algae coexisting within limited areas on rocky shores.

67. Sammarco, P.W. 1980. *Diadema* and its relationship to coral spat mortality: grazing, competition, and biological disturbance. *Journal of Experimental Marine Biology and Ecology* 45: 245-272.

Diadema antillarum densities (0-64 urchins/m^2) were manipulated by the use of enclosures in Discovery Bay, Jamaica, to compare the grazing under primary and post-primary succession conditions. An inverse relationship was noted between algal percent cover and *Diadema* density. Highest levels of coral recruitment and diversity occurred on exposed microhabitats despite the high algal cover since the *Diadema* densities were low. Later, intense competition for light and space between algae and coral resulted in high coral mortality rates. The surviving coral spat was located in cryptic and protected environment. Furthermore, competition from sessile epifauna and –flora communities and high sedimentation rates further depressed coral recruitment and survival. Intermediate levels of all influences on the coral community allowed optimal conditions for coral survival.

68. Schiel, D.R. 1982. Selective feeding by the echinoid, *Evechinus chloroticus*, and the

removal of plants from subtidal algal stands in northern New Zealand. *Oecologia* 54: 379-388.

Two field-based and one laboratory based experiments were conducted to investigate the feeding choice of echinoid *Evechinus chloroticus* for six fucoid and one laminarian species of algae. The results ranked *Ecklonia radiata* as the most highly preferred algae. The evidence suggested that feeding preferences of echinoids do not clearly exert the major influence on the removal of plants from natural stands. Preference as determined from the ranking in the experiment is only the one factor affecting the removal of algae by echinoid. The other factors that need to be investigated are density of echinoids, algal susceptibility to removal and the distribution and abundances of the various algal species and echinoids relative to each other. It is also suggested that algal life history attributes may be unaffected by echinoids and that coevolutionary arguments may not be appropriate for describing echinoid-algal interactions.

69. Steneck, R.S. 1983. *Quantifying herbivory on coral reefs: just scratching the surface and still biting off more than we can chew.* Pp. 103-111 In: M.L. Reaka, ed. The ecology of deep and shallow coral reefs. Symposia series for undersea research. Vol.1. Office of Undersea Research. NOAA. Rockville, Maryland, USA.

Six different techniques were simultaneously used to quantify herbivory on the Caribbean Island of St. Croix. Functional groups based on shapes

and structural properties of the algae and feeding capabilities of herbivores were assigned in order to study their diverse assemblages. Highest herbivory was recorded for shallow fore-reef sites mostly from fish, limpets, and urchins. Herbivory from all sources decreased in backreef, shallow algal ridge, and deep wall-reef habitats. Latter sites recorded the lowest grazing levels. *Thalassia* bioassay techniques aided in assessing herbivory on macrophytes but it gave contradictory results to other techniques.

70. Vadas, R.L. 1977. Preferential feeding: An optimization strategy in sea urchins. *Ecological Monographs* 47: 337-371.

Feeding preference of *Strongylocentrotus drobachiensis, S. franciscanus* and *S. purpuratus* was monitored for various algal families. The reasons for their preference and dislike were also explained. An inverse relationship existed between food preferences and caloric content of algae. Absorption efficiencies for the three urchins were strongly correlated with food preference rankings. Mean values for the three species ranged from 84-91% on *Nereocystis,* 77-83% on *Costaria*, 64-78% on *Laminaria saccharina*, 62-71% on *Callophyllis flabellulata*, 28-56% on *Monostroma fuscum*, 40-56% on *Agarum. cribrosum* and 36-52% on *A. fimbriatum*. Diets were switched and difference e.g. sizes (diameter and weight), gonad weights etc. noted according to the ranks switched. Qualitative and quantitative (density, frequency percentage, relative biomass) measures of algal availability were measured in detail. Furthermore, descriptions of the opportunistic strategies that algae and urchins have evolved to survive well have been pointed out using models.

71. Valentine, J.F. and L.H. Jr Kenneth. 1991. The role of sea urchin grazing in regulating subtropical seagrass meadows: evidence from field manipulations in the northern Gulf of Mexico. *Journal of Experimental Marine Biology and Ecology* 154: 215-230.

Sea urchin herbivory is known to influence kelp forest distributions and this article materialized this belief. Sea urchin densities were manipulated in St. Joseph Bay, Florida. Lower densities of *Lytechinus variegatus* (L.) was investigated to overgraze *Thalassia testudinum* meadows (approximately 20 individuals/m^2) during winter and higher densities (approximately 40 individuals/m^2) during summer and fall. Hence, this documentation of seasonal impact proved sea urchin herbivory important in regulating subtropical seagrass meadow biomass and size especially where urchin densities exceeded 20 urchins/m^2.

COMMUNITY STRUCTURE

72. Andrew, N.L. and A.B. MacDiarmid. 1991. Interrelationships between sea urchins and spiny lobsters in northeastern New Zealand. *Marine Ecology Progress Series* 70: 211-222.

The interrelation between the sea urchin *Evechinus chloroticus* and the spiny lobster *Jasus edwardsii* was investigated in the shallow subtidal zone of rocky reefs in northern New Zealand. The movement patterns of lobsters indicated that the urchins were more vulnerable to nocturnally foraging lobsters. Laboratory experiments demonstrated that large lobsters ate all sizes of urchins while all sizes of lobsters ate small sea urchins (< 50mm test diameter) in preference to larger ones. The presence of edible gastropods and large brown algae did not cause larger sea urchins to be eaten. The removal of brown algae, sea urchins and the gastropods did not cause significant reduction in the daytime density of *J. edwardsii*. Necessary experiments are discussed to argue that differing microhabitat requirements of the 2 species mean that large abundances of *E. chloroticus* are unlikely to depress *J. edwardsii* densities.

73. Bak, R.P.M., M.J.E. Carpay and E.D. de Ruyter van Steveninck. 1984. Densities of the sea urchin *Diadema antillarum* before and after mass mortalities on the coral reefs of Curacao. *Marine Ecology Progress Series* 17: 105-108.

The mass mortality of *Diadema antillarum* on the Caribbean reefs has spread from the Curacao harbour mouth along the coast, most rapidly advancing in the down-current direction. The sea urchins used to occur in densities sufficiently high enough to influence the composition and growth of reefs. Hence, their removal has a pronounced effect on the carbonate budget. Recruitment continues on the affected reefs and in the direction up current.

74. Breen, P.A. and K.H. Mann. 1976. Changing lobster abundance and the destruction of kelp beds by sea urchins. *Marine Biology* 34: 137-142.

Implications for management are discussed for a study area in Nova Scotia, Canada where the lobster *Homarus americanus* decreased by 50% in 14 years. This lobster is a chief predator of sea urchins, *Strongylocentrotus droebachiensis* who have destroyed 70% of the *Laminaria spp*. beds in 6 years.

75. Carpenter, R.C. 1985. Sea urchin mass-mortality: Effects on reef algal abundance, species composition and metabolism and other coral reef herbivores. *Proceedings of the Fifth International Coral Reef Congress*, Tahiti 4: 53-60.

The impact of grazing of algal communities by *Diadema antillarum* was investigated. Majority of the data was obtained using inclusion-exclusion cage experiments and similar results to other research were revealed. The mass mortality of *Diadema* in the Caribbean provided a natural test of many of the experimental hypotheses. Using two years of pre-mortality data, the impact of *Diadema* removal was assessed. Its removal was observed to cause shifts in algal abundance, species composition and metabolism. Hence, *D. antillarum* is strongly seen as an instrument for structuring many Caribbean coral reef algal communities.

76. Carpenter, R.C. 1990. Mass mortality of *Diadema antillarum* i. Long-term effects

on sea urchin population dynamics and coral reef algal communities. *Marine Biology* 104: 67-77.

This paper discusses the aftermath of *Diadema antillarum* mass mortality in 1983/1984 in relation to alterations in the sea urchin density and the biomass, species composition, and rates of primary productivity of algal communities at several study sites in St. Croix, U.S. Virgin Islands. A second, less severe mortality event occurred in October 1985, which reduced the urchin levels even more. Consequently, *D. antillarum* recruitment rates decreased resulting in population densities 2-30% of their premortality levels and algal biomass increased by 22-439% across reef zones 16 months after the die-off. The algal community response was in good correlation to the urchin densities prior to the mortality. There were major algal shifts observed in algal species. Premortality times recorded dominating algal turfs and crustose algae while macroalgae was rare or absent. This got switched by 40% algal turf and 47% macroalgae after 25 months of mass mortality. The high biomass of inedible macroalgae gets dislodged by storms and waves and transported to adjacent communities reflecting a transition from a grazing-based food web to an area void of primary production.

77. Carpenter, R.C. 1990. Mass mortality of *Diadema antillarum* ii. Effects on population densities and grazing intensity of parrotfishes and surgeonfishes. *Marine Biology* 104: 79-86.

The mass mortality of *Diadema antillarum* in February 1984 provided a good basis for testing the hypothesis that herbivorous fishes and *D. antillarum* compete for benthic algae as their major source of food. Visual censuses of herbivorous fishes conducted on the 4 reef zones of Tague Bay Reef, St. Croix, U.S. Virgin Islands over a 4 year period before and after the die-off indicated a 3-fold increase in backreef and shallow (2m) forereef zones and 2-fold and 4-fold in mid (5m) and deep (10m) forereef zones, respectively. Juvenile parrotfishes constituted the increase except in the shallow forereef where acanthurids were most abundant. Since the grazing intensity by fishes increased in three of the four reef zones immediately after the mass mortality, there is enough support for the hypothesis that exploitative competition for algal resources was present prior to the death. However, the alternative hypothesis cannot be completely discounted. Despite increase in grazing intensity of herbivorous fish and sea urchin loss, algal cover and biomass continued to grow and contribute to the reef community structure.

78. Glynn, P.W., G.M. Wellington and C. Birkeland. 1979. Coral reef growth in the Galapagos: limitations by sea urchins. *Science* 203: 47-49.

Eucidaris thouarsii, a regular echinoid, are seen grazing openly on coral reefs both day and night. They occur in larger sizes on the Galapagos Island compared to Panama and mainland Ecuador populations. This is attributed to intense predation from fishes on the mainland compared with the island batch. An erosion-accretion assessment revealed that *Eucidaris* in the Galapagos were interfering with the growth of pocilloporid reef frame.

79. Harrold, C. and D.C. Reed. 1985. Food availability, sea urchin grazing and kelp forest community structure. *Ecology* 66, no.4: 1160-1169.

These authors discuss the kelp forest community on the west end of San Nicolas Island, California, as a dynamic patchwork of barren areas characterized by grazing sea urchins and an algal assemblage consisting of upright and encrusting coralline algae, and kelp-dominated area characterized by high densities of perennial brown algae. This study examined factors that regulated the grazing activity of sea urchins (*Strongylocentrotus franciscanus*), which in turn determines the structure of this community. The barren area consisted of sparse drift algae and poorly nourished sea urchins occupied open and unprotected habitat and actively grazing the substratum. The kelp-dominated area had abundant drift algae, well nourished sea urchins that moved little, occupied cracks and crevices and possibly fed on drift algae. Earlier in the study, both areas commenced with a kelp-dominated area whereby one later transformed to a barren. This paper discusses a qualitative model where the switch from one configuration to another is triggered by a behavioural switch in the mode of feeding of the red sea urchins. Other confounding variables such as availability of drift algae, abundance of attached algae and hydrographic conditions, also triggers this switch. The authors introduce a new view on the functioning of a kelp forest.

80. Hughes, T.P., C.R. Daniel and M.J. Boyle. 1987. Herbivory on coral reefs: community structure following mass mortalities of sea urchins. *Journal of Experimental Marine Biology and Ecology* 113: 39-59.

The impact that catastrophic mortalities of *Diadema antillarum* (1983) had on the community structure of Jamaican coral reefs was investigated. Algal abundance increased up to a mean of 95% cover, coral cover was reduced by as much as 60% by competition with algae, *D. antillarum* densities within 10 sites ranged from 0-12% pre-1983 levels and herbivorous fishes remained at relatively low levels due to overfishing. With low numbers of sea urchins and herbivorous fish, the current state of community structure may prevail for long.

81. Keesing, J.K. 1992. Influence of persistent sub-infestation density *Acanthaster planci* (L.) and high-density *Echinometra mathaei* (de Blainville) populations on coral reef community structure in Okinawa, Japan. *Proceedings of the Seventh International Coral Reef Symposium,* Guam 2: 769-779.

A survey on the Okinawan reef outlines the severe impact *Acanthaster planci* are having on the community structure of the reefs. Prior to the outbreaks of *A. planci* in early 1970’s and 1980’s reefs exhibited *Acropora* dominance. The selective feeding preference of *A. planci* is drastically reducing the reef community structure. The reef community examined was dominated by *Porites* (27%), *Millepora* (30%) and alcyoniid soft corals (30%) compared with acroporids (0.6%) and pocilloporids (0.2%). The acroporids and pocilloporids are so highly favoured by *A. planci* that their predation rates are 27 and 53 times their areal abundance. Most of the *Acropora* recruits (greater than or equal to 3cm diameter) had predation scars. The combined effect of *A. planci* and *E. mathaei* are strongly declining the coral community structure via their selective feeding preferences and bioerosion rates, respectively which may give rise to large non-preferred species.

82. Levitan, D.R. 1988. Algal-urchin biomass responses following mass mortality of *Diadema antillarum* Philippi at Saint John, U.S. Virgin Islands. *Journal of Experimental Marine Biology and Ecology* 119: 167-178.

An impact assessment was conducted in Lameshur Bay, Saint John, U.S. Virgin Islands in regards to the mass mortality (95-99%) of *Diadema antillarum* in 1983. The survey covered 6 months before and 6, 12, 18, 26, 30 and 42 months after the disaster. It took a closer look at the *Diadema* population and body size and algal biomass displacements.

83. Levitan, D.R. 1992. Community structure in times past: influence of human fishing pressure on algal-urchin interactions. *Ecology* 73, no.5: 1597-1605.

This paper outlines the method by which the demipyramid length and the test diameter ratio of the sea urchin, *Diadema antillarum* were utilized to assess the food availability conditions. With the baseline data available, it can be used to investigate the algal abundance and biotic interactions in the past. Experimental manipulations on food conditions and urchin densities provided data that was compared with museum specimens collected over the past 100 years from 30 locations in the Caribbean. The relative demipyramid lengths from the museum were also compared over time with human population density, human fishing pressure and geographic region. The results showed an indirect influence on demipyramid size by human activity, which varied geographically. This suggests that the Caribbean coral reef structure may be influenced by predator-herbivore interactions. However, the natural variation in demipyramid sizes needs to be considered before making generalizations about human impact.

84. McClanahan, T.R., A.T. Kamukuru, N.A. Muthiga., M.G. Yebio and D. Obura. 1996. Effect of sea urchin reductions on algae, coral and fish populations. *Conservation Biology* 10, no.1: 136-154.

Three Kenyan coral reef lagoons were monitored seven times for sea urchin reduction experiments over a year period. The study concentrated on the influence of reductions in sea urchin populations on coral, algae and fish populations. Control and experimental sea urchin reduction plots

(50m x 50m) were assessed for wet weight census and population density dynamics. Generally, sea urchin reduction plots showed an increase in algal cover, fisheries populations and species richness and diversity of corals. Sea urchin reduction experiments are recommended for severely degraded reefs or reefs experiencing less fishing effort and will help restore fish numbers, feeding importance, species diversity and fisheries production.

85. McClanahan, T.R. and J.C. Mutere. 1994. Coral and sea urchin assemblage structure and interrelationships in Kenyan reef lagoons. *Hydrobiologia* 286: 109-124.

This article presents a summary of hard coral and sea urchin assemblage structure (species richness, diversity and abundance) on various Kenyan coral reef lagoons, which were subject to varying human resource use. The Malindi and Watamu Marine National Parks were exposed to tourist but protected from fishing and coral collection. Mombasa MNP was unfished for a year but was exploited for fish and coral prior to protection hence was declared ‘transitional reef’. Vipingo, Kanamai and Diani reefs were completely unprotected. The protected and unprotected reefs showed distinct coral assemblage patterns. Protected reefs had slightly higher ($p<0.01$) coral cover (23.6 +/- 8.3% +/- S.D.) and higher coral species richness and diversity than unprotected reefs (16.7 +/- 8.5), but the transitional reef had the highest coral cover (30.8 +/- 6.4) largely attributable to large *Porites* collection. This reflected high species richness but low diversity for transitional reef. Also, coral community assemblage declined with effect to increasing sea urchin assemblage and diversity. However, the relative abundance of *Porites* increased with sea urchin abundance. Hence, direct and indirect human resource use is strongly seen to influence the reef topographic complexity.

86. McClanahan, T.R. and N.A. Muthiga. 1988. Changes in Kenyan coral reef community structure and functions due to exploitation. *Hydrobiologia* 166: 269-276.

Reefs of different histories and fishing exploitation levels were compared in Kenya and exploited reefs reported greater sea urchin densities and sizes, fewer and smaller fish and reduced coral cover. *Echinometra mathaei* counted a biomass incline of 5 fold in 15 years. *E. mathaei*, *Diadema savignyi* and *D. setosum* were most abundant on reefs reflecting their ability to escape predation and competitors by occupying different sizes of burrows and crevices in the lagoon. The most exploited reef demonstrated a nearly monospecific barren of *E. mathaei* living outside burrows. Their release as a top competitor for space led to decrease in coral cover, increased bioerosion, loss of topographic complexity, species diversity, fish biomass and utilizable fisheries productivity. Fisheries from the outer reef edges are more likely structured by the stresses from waves and currents.

87. McClanahan, T.R. and S.H. Shafir. 1990. Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. *Oecologia* 83: 362-370.

    Six reefs, two protected and four unprotected were studied in Kenyan reef lagoons to assess and compare the differences in community structure of sea urchins and finfish which was attributable to removal of finfish predators via overfishing. More specifically, the study attempted to determine (1) the major sea urchin and finfish predators, (2) the effect of predation on sea urchin community structure and, (3) the possible effect of sea urchin increases and finfish decreases on the lagoonal substrate. Measurable parameters, which aided in answering the above questions were sea urchin and finfish abundance and diversity, substrate cover diversity and complexity. Statistical manipulations were used to make separate conclusions for protected and unprotected reefs.

88. Miller, R.J. 1985. Succession in sea urchin and seaweed abundance in Nova Scotia, Canada. *Marine Biology* 84: 275-286.

    This article is a mere account of the succession of sea urchin and seaweed abundance that has occurred on Nova Scotia shorelines since the mass mortalities of *Diadema antillarum*. In the 1 to 2 years following the event seaweed cover and occurrence increased significantly for all of five categories of wave exposure and for six of seven algal taxa respectively.

Three locations demonstrated recovering urchin populations but another disease tragedy further reduced the population. The urchins have developed a very low resistance to disease, presumably a secondary impact of catastrophic mortality.

89. Ogden, J.C. and P.S. Lobel. 1978. The role of herbivorous fishes and urchins in coral reef communities. *Environmental Biology of Fishes* 3, no.1: 49-63.

Fish and sea urchins are conspicuous herbivores of coral reef ecosystems and this research attempts to reveal the impact their foraging activities are having on the distribution and abundance of algae and how their exertion contribute to the coral community structure and shifts associated with it.

90. Prince, J. 1995. Limited effects of the sea urchin *Echinometra mathaei* (de Blainville) on the recruitment of benthic algae and macroinvertebrates into intertidal rock platforms at Rottnest Island, Western Australia. *Journal of Experimental Marine Biology and Ecology* 186: 237-258.

While many species of urchins have been a factor controlling the subtidal community structure, *Echinometra mathaei* has shown a much less effect on the intertidal community. *E. mathaei* densities were manipulated to observe the limiting effect it has on the recruitment of particular species of macroalgae or macroinvertebrates. Though many sites have revealed some effects of urchin removal, no ‘keystone’ effect was quite seen.

91. Sammarco, P.W. 1982. Echinoid grazing as a structuring force in coral communities: Whole reef manipulations. *Journal of Experimental Marine Biology and Ecology* 61: 31-55.

Shallow water coral community structure was studied by initially removing entire populations of *Diadema antillarum* (> 3000 urchins), then 6 months later remaining regular echinoids (> 7000 urchins) from a patch reef in Discovery Bay, Jamaica. *Diadema* demonstrated uniform grazing while *Echinometra* grazing was highly patchy. Adult coral percent cover increased in the presence of *Echinometra viridis* while it decreased in the absence of all echinoid grazing simply due to massive overgrowth of algae. Coral recruitment declined in *Diadema* presence due to disturbance from it's feeding activities, unlike *E. viridis*. Coral diversity maximized when all echinoids were present, intermediate in the presence of *E. viridis* (without *Diadema*) and lowest in the absence of all echinoids. Predation resulting from *Echinometra* and *Diadema* was responsible for damaging larger coral colonies, especially *Porites*. Alteration of echinoid species composition reflected a shift in species composition of benthic algae and associated invertebrates. An inventory of invertebrate community was assessed to mark the shift.

92. Sammarco, P.W., J.S. Levinton and J.C. Ogden. 1974. Grazing and control of coral reef community structure by *Diadema antillarum* Philippi (Echinodermata: Echinoidea): A preliminary study.

These authors attempted to show the possible impact *Diadema antillarum* could have on the epifaunal community structure. Overall, the elimination of this urchin from a patch reef in St. Croix, U.S. Virgin Islands resulted in huge increase in macro-algal biomass, alterations in species composition, shifts in dominance, an increase in species numbers and a decrease in equitability. The disturbance from the urchin activity largely disrupts virgin coral substrates.

93. Tegner, M.J. and L.A. Levin. 1983. Spiny lobsters and sea urchins: analysis of a predator-prey interaction. *Journal of Experimental Marine Biology and Ecology* 73: 125-150.

Predatory spiny lobster, *Panulirus interruptus* (Randall) consume two species of sea urchins, *Strongylocentrotus franciscanus* (A. Agassiz) and *S. purpuratus* (Stimpson), the two major herbivores in southern California kelp forest communities. Aquarium experiments indicate that *P. interruptus* prefers *S. purpuratus* to *S. franciscanus* of comparable size hence explaining the higher mortalities of the former in the field. Juvenile *S. franciscanus* (<60mm-test diameter) are preferred over the larger urchins while the smallest (<30mm TD) seeks refuge under spine canopy. Mid-sized form the biggest proportion of lobster diet. The large (>90mm TD) *S. franciscanus* are the least predated due to handling complexities. Factors such as relative movement, spine length, test thickness, and gonad weights of sea urchins were examined to evaluate reasons for lobsters' choice of prey. Moreover, lobster behaviour was monitored to assess urchin availability to these predators. This selection of urchin sizes is probably responsible for the bimodal size-frequency distribution seen *in S. franciscanus* populations in areas where these predators are common. The heavy fishing pressure has resulted in the release of sea urchin populations and consequent episodes of destructive grazing in the 1950’s and following years.

94. Wharton, W.G. and K.H. Mann. 1981. Relationship between destructive grazing by the sea urchin, *Strongylocentrotus droebachiensis*, and the abundance of American lobster, *Homarus americanus*, on the Atlantic coast of Nova Scotia. *Canadian Journal of Fish and Aquatic Sciences* 38: 1339-1349.

Authors of this paper aim to assimilate information on the relationship between lobsters and other predators, sea urchins and kelp and form a coherent theory on how the change in each of the population affects the other. The relationships between percentage cover of macroalgae, population structure of sea urchins (*Strongylocentrotus droebachiensis*) and the history of American lobster (*Homarus americanus*) fishery were examined at 9 sites along the Atlantic coast of Nova Scotia from Guysborough Country in the northeast to Pubnico in the southwest. After assessing the three factors in all sites it was concluded that a critical decline in lobster catches resulted from kelp bed destruction.

ANTHROPOGENIC INFLUENCES

95. McClanahan, T.R and D. Obura. 1997. Sedimentation effects on shallow coral communities in Kenya. *Journal of Experimental Marine Biology and Ecology* 209: 103-122.

Empirical studies on the influence of sediment discharge in the Watamu and Malindi National Marine Parks were conducted. Total algal cover increased, soft coral and sponge cover were higher at increasing levels of sediment, coral cover increased for reefs experiencing intermediate levels of sediment when compared with the low or high-sediment influenced. Positive correlation between differences in coral genus abundance and differences in mean coral colony sizes over time and among reefs suggest development of a suite of sediment-tolerant (*Echinopora, Galaxea, Hydnophora, Millepora,* and *Platygyra*) and sediment-intolerant (*Favia, Montipora,* and *Pocillopora*) genera. *Acropora, Astreopora, Favites,* and *Porites* were intermediate between the two groups.

96. Smith, A.K., P.A. Ajani and D.E. Roberts. 1999. Spatial and temporal variation in fish assemblages exposed to sewage and implications for management. *Marine Environmental Research* 47, no.3: 241-260.

This article utilized underwater visual surveys involving a Before/ After/ Control/ Impact (BACI) experimental design to elucidate the impact sewage effluent from a deepwater outfall was having on the abundance and species richness of temperate rocky reef fishes and the abundance of sea urchins. Multivariate analysis pointed out decline in fish assemblages at the outfall and control locations while the univariate analysis indicated a variation of abundance and richness of groups of fish and individual species over times, periods and locations. Hence, the effluent levels were concluded to have an impact on the fish and urchin populations and were outside the pollution management guidelines.

REPRODUCTION ECOLOGY

97. Drummond, A.E. 1995. Reproduction of the sea urchins *Echinometra mathaei* and *Diadema savignyi* on the South African Eastern Coast. *Marine Freshwater Research* 46: 751-755.

Reproductive cycles of *Echinometra mathaei* and *Diadema savignyi* were investigated through gonad indices and histological procedures on the South African eastern coast. Results revealed that both species spawned annually during summer months (December to March-April). Gametogenesis within and between sexes of *D. savignyi* demonstrated strong synchrony with repeated occasions of spawning monthly unlike *E. mathaei* which showed poor synchrony and continuous spawning.

98. Gonor, J.J. 1972. Gonad growth in the sea urchin, *Strongylocentrotus purpuratus* (Stimpson) (Echinodermata: Echinoidea) and the assumptions of gonad index methods. *Journal of experimental Marine Biology and Ecology* 10: 89-103.

A study was carried out on the gonad ratios of *Strongylocentrotus purpuratus* in central Oregon intertidal populations. The findings revealed that these urchins begin to produce gametes at a diameter of 25mm during the second year of their lives. All individuals above 40mm have mature gametes during the mid-winter spawning season. The gonad size to body size increases rapidly till ~ 45mm and is at its maximum between ~ 40-50mm. Thereafter, the ratio drops slightly with increasing size. Populations were compared for body proportions, ratio of gonad to body sizes and the consistency of differences. The differences were explained by variations in food supply in different habitats. The use of gonad ratio methods assumes that animals of different body size have the same ratio of gonad size to body size and this is not true for four species of urchins. This assumption only works for animals of the same size through time within a population or from different habitats.

99. Levitan, D.R., Sewell, M.A. and Chia, F. 1992. How distribution and abundance influence fertilization success in the sea urchin *Strongylocentrotus franciscanus*. *Ecology* 73, no.1: 248-254.

A detailed investigation was conducted at a depth of 9m on the west coast of Vancouver Island, British Columbia, Canada on the exact spawning group size, degree of aggregation, position within an aggregation and water flow affecting success of in situ fertilization for the sea urchin *Strongylocentrotus franciscanus*. Populations were simulated with gametes and placed at certain distant arrays to assess the fertilization success rates, which ranged from 0-82%. Large group size with more aggregation, decrease in flow velocity and central and downstream positions within an aggregation led to higher fertilization success. Hence, the survival of an individual urchin is dependent upon the combination of population parameters and environmental factors.

100. Phillips, B.F. and J.S. Pearse. 1968. Continuous reproduction in the Indo-Pacific sea urchin *Echinometra mathaei* at Rottnest Island, Western Australia. *Australian Journal of Marine Freshwater Research* 19: 161-172.

Eleven gonadal samples of *Echinometra mathaei* from Rottnest Island, Western Australia were examined and analyzed histologically. All stages of gametogenesis were detected in most samples but little seasonal change in reproductive activity could be noticed. All samples showed mature gametes but lack of synchrony among individuals hence reflecting continuous spawning. This is presumably due to high sea temperatures even in winter, which could induce continuous reproduction.

101. Wahle, R.A. and S.H. Peckham. 1999. Density-related reproductive trade-offs in the green sea urchin, *Strongylocentrotus droebachiensis*. *Marine Biology* 134: 127-137.

A series of reproduction-oriented experiments were undertaken in response to the rapidly depleting populations of *Strongylocentrotus* *droebachiensis* in the Gulf of Maine. Population surveys and fertilization experiments were used to evaluate the opposing effects of varying population densities on gonad development and fertilization success. Gonad indices were determined over a range of population densities (0.1-250 ind. m^{-2}) at depths 5m and 15m at seven sites. High urchin densities in shallow areas recorded a 50% decline in gonad indice while the deeper areas showed a consistently low gonadal mass, which did not vary significantly with density. Since macroalgae cover covaried inversely with sea urchin density, further experiments were designed to determine the interaction between sea urchin density and kelp canopy on fertilization success. Data recorded demonstrated (1) fertilization rate decreased faster than individual gamete production at the same density, and (2) kelp enhanced fertilization success at high densities as long as the egg was 25cm within a sperm source. Additional laboratory experiments revealed that diluted sperm, at an ambient temperature of 3-5 ^{0}C were viable for < 1 h while the egg viability was unchanged for > 8 h.

POPULATION DYNAMICS

102. Clark, A.M. 1976. *Echinoderms of coral reefs. Biology and geology of coral reefs.* O.A.E. Jones, R. New York. Academic Press. 111: Biology 2.

This book chapter reviews all classes of Echinoderms, Asteroidea, Echinoidea, Ophiuroidea, Holothuroidea and Crinoidea in terms of individual ecological events of their life cycle. These include patterns of distribution, abundance, density, morphology, predation, behaviour, feeding requirements and habitat preferences.

103. Cole, R.G. and D. Keuskamp. 1998. Indirect effects of protection from exploitation: patterns from populations of *Evechinus chloroticus* (Echinoidea) in northeastern New Zealand. *Marine Ecology Progress Series* 173: 215-226. Predator influence on the sea urchin *Evechinus chloroticus* was investigated in northeastern New Zealand by comparing densities, population size structure, and crevice occupancy in both marine reserves and exploited areas. Overall sea urchin density did not differ between the two locations, however the population size structure were generally more bimodal in the protected area. Size-related patterns of crevice occupancy did not vary consistently between protected and exploited locality pairs. Cape Rodney – Okakari Point (CROP) Marine Reserve showed the most pronounced effects of protection where relative to the adjacent fished areas (1) sea urchin densities were ~ 3 times lower, (2) size structures were more bimodal, and (3) larger sea urchins (~40mm test diameter) were crevice-bound. Transplant experiments on sea urchins 30-40mm (TD) showed higher losses at a protected site than a fished locality. Test weight records of adult sea urchins were higher in the protected area than the unprotected and this was attributed to larger and more numerous predatory fishes in the reserve. A strong bimodal size structure persisted and sea urchin densities declined over 10 years at a site in CROP Marine

Reserve. Hence, it is suggested that generalizations made from reserves for exploited areas could prove erroneous.

104. Cowen, R.K. 1983. The effect of sheephead (*Semicossyphus pulcher*) predation on red sea urchin (*Strongylocentrotus franciscanus*) populations: an experimental analysis. *Oecologia* (Berlin) 58: 249-255.

An experimental evaluation was performed on San Nicolas Island, California in Sept. 1980 where all (N=220) sheephead (*Semicossyphus pulcher*) were removed from an area of approximately 12,700 m^2 and subsequent changes in sea urchin (*Strongylocentrotus franciscanus*) numbers and microhabitat utilization were monitored over permanent transects for two years. *In situ* measurements were taken for size-frequency distribution of the sea urchin population. Although the sea urchin ranked seventh in the sheephead's diet on San Nicolas Island, there had been significant (26%/year) increase in sea urchin population in the experimental area, but no change was observed in the control site. Also, a higher proportion of sea urchins were observed on the exposed versus sheltered microhabitats in the removal sites. Not much change was observed in the size-frequency distribution of urchins possibly due to an observation period of an year. The distribution was unimodal and skewed to the left, implying weak recruitment of urchins. Comparative assessments of other exposed areas demonstrated that where sheephead densities were high, urchins were hidden and where the densities were low, sea urchins were found exposed. Hence, this study implies that sheephead densities are capable of regulating the density and microhabitat distribution of sea urchin populations. Other factors affecting sea urchin populations are also discussed.

105. Ebert, T.A. 1965. A technique for the individual marking of sea urchins. *Ecology* 46, no.1 and 2: 193-194.

A marking technique has been devised to monitor the individual growth of purple sea urchin, *Strongylocentrotus purpuratus* on the Oregon coast. Though it has been used on urchins only, with slight modifications it can be used generally. Dyes and tagging methods are unreliable methods. This method consists of inserting 0.25mm diameter nylon monofilament line through two holes in the test, marking the line with coloured pieces of vinyl tubing, and fastening the ends of the line together to form a loop. Regeneration rates around the holes are measured.

106. Ebert, T.A. 1968. Growth rates of the sea urchin *Strongylocentrotus purpuratus* related to food availability and spine abrasion. *Ecology* 49, no.6: 1075-1091.

A survey of purple sea urchin population, *Strongylocentrotus purpuratus* was undertaken at the Sunset Bay, Oregon and variations were noted in the size-frequency distributions of three sub-populations. This was attributed to two environmental components, the ‘weather’, which broke spine, and food availability and consumption.

107. Ebert, T.A. 1973. Estimating growth and mortality from size data. *Oecologia* 11: 281-298.

This paper presents a method whereby growth and mortality rates of a variety of populations can be approximated on the basis of average individual size at two times during a year. This model assumes a constant rate of mortality, Brody-Bertalanffy growth, a stationary age distribution and recruitment confined to one month each year. A hypothetical example is used to show the interactions between growth and mortality constants, size at recruitment, asymptotic size and average individual size. Data from literature was utilized to discuss three examples, flathead sole (*Hippoglossoides elassodon*), sea urchin (*Echinus esculentus*) and the crown-of-thorns-starfish (*Acanthaster planci*) applying the model.

108. Ebert, T.A. 1982. Longevity, life history, and relative body wall size in sea urchins. *Ecological Monographs* 52, no.4: 353-394.

Thirty-eight populations of seventeen species of sea urchins in the Indo-West Pacific were studied for relative size of the body wall and exposure to the surf. Dissections of live animals helped determine the size of body components. Values from the experiments were used to calculate Richard’s growth function, mortality coefficient and annual survival probability. Survivorship increased with relative size of the body wall and with increased protection from surf. The positive relationship between survival probability and relative body wall size supports the hypothesis that survival is related to allocation of resources to maintenance.

109. Ebert, T.A. and M.P. Russell. 1993. Growth and mortality of subtidal red sea urchins (*Strongylocentrotus franciscanus*) at San Nicolas Island, California, USA: problems with models. *Marine Biology* 117: 79-89.

Red sea urchins, *Strongylocentrotus franciscanus* were tagged with tetracycline for two years in 1990 to study the growth rates at subtidal sites off San Nicolas Island, California. A trend of initial slow growth then maximum rate and a final prolonged slow growth was observed. Survival rates differed in the context of assumptions whereby it was 71-77% /yr if the population was assumed to be stable and stationary and 79-86% / yr otherwise. Analysis of transitions in the size distributions from 1990 to 1991 suggested that annual survival may have been size specific: 91% /yr for 1.1-4.0cm diameter, 82% /yr for 4.1-7.0cm diameter, and 63% /yr for those from 7.1-10.0cm diameter. Alternatively, size-specific immigration could explain the size-specific survival observed.

110. Forster, G.R. 1959. The ecology of *Echinus esculentus* (L.) quantitative distribution and rate of feeding. *Journal of Marine Biological Association. U.K.* 38: 361-367.

A diving operation done on a rocky area just west of Tinker Shoal was used to explore *Echinus* populations. Their numerical density and rate of algal browsing was monitored carefully. Some comparative tests on the browsing behaviour were made in the aquarium tanks. This paper gives a detailed account of the new techniques used to carry out the above measurements.

111. Keats, D.W., G.R. South and D.H. Steele. 1984. Ecology of juvenile green sea urchins (*Strongylocentrotus droebachiensis*) at an urchin dominated sublittoral site in eastern Newfoundland. *Proceedings of the Fifth International Echinoderm Conference*, Galway 1: 295-302.

The population structure of *Strongylocentrotus droebachiensis* was examined over 5 years in an urchin dominated site in eastern Newfoundland. The distribution of juveniles was the main focus in relation to depth, inter-annual variation and microhabitats. Juvenile urchin densities were lower at depths of 0-2m and 12m below MLW with abundant macroalgae but higher in the barrens that occur at intermediate depths. The urchins occurred in higher numbers in some years only reflecting the high predation rates on juveniles. The cryptic microhabitats allow survival of these larger urchins whose grazing maintain the barrens.

112. Khamala, C.P.M. 1971. Ecology of *Echinometra mathaei* (Echinoidea: Echinodermata) at Diani Beach, Kenya. *Marine Biology* 11: 167-172.

An in depth study was done on the population dynamics of *Echinometra mathaei* at Diani beach on the Kenyan coast. The research involved assessment of distribution, density and behaviour within transects that ran on two reefs for April, June and September. Measurements of urchin sizes and their movement, gregariousness, homing and feeding data were collected for the inner and outer reef positions. *E. mathaei* occurred exposed on seaweeds in the inner reef and cryptic in crevices in the outer reef. Modal values from size-frequency distributions aided in estimating their growth and revealed smaller individuals in the inner reef and larger ones on the outer zone. *E. mathaei* demonstrated a sedentary behaviour.

113. Lessios, H.A. 1988. Population dynamics of *Diadema antillarum* (Echinodermata: Echinoidea) following mass mortality in Panama. *Marine Biology* 99: 515-526.

A long-term monitoring study was undertaken after the mass mortality of *Diadema antillarum* throughout the Caribbean Sea and the western Atlantic Ocean. Its population dynamics was traced from 1983 to 1987 and recruitment was observed only to the 1-1.5cm class. Other species of urchins did not show a clear pattern of increase since the demise of *D. antillarum*. Two reefs where *Echinometra viridis, Eucidaris tribuloides* and *Lytechinus williamsi* were removed showed no significant differences in recruitment of *D. antillarum* relative to two other reefs where these species occurred at natural densities. Though *D. antillarum* produced gametes with the same per capita intensity and lunar synchrony as before, low population densities prevailed. Low probability of fertilization and lack of recruitment was attributed to low numbers of reproducing adults.

114. Lessios, H.A., B.D. Keesing, G.M. Wellington and A. Graybeal. 1996. Indo-Pacific echinoids in the tropical eastern Pacific. *Coral Reefs* 15: 133-142.

Genetic investigations were used to confirm that echinoid faunas from Isla del Coco, Clipperton and Revillagigedos are a mixture of biogeographic provinces. Evidence from isozymes, and mitochondrial DNA sequences indicate that the Indo-Pacific echinoids are a compliment of east and west Pacific species. Hence, the East Pacific Barrier may not be an obstacle to migration as thought previously.

115. Levitan, D.R. 1989. Density-dependent size regulation in *Diadema antillarum*: effects on fecundity and survivorship. *Ecology* 70, no.5: 1414-1424.

Diadema antillarum has evolved a life history strategy where it regulates its size thus increasing survivorship and reproductive output under fluctuating conditions of population density and resource availability. Cage experiments both in the field and laboratory involving different densities and sizes of urchins were monitored with different levels of food supplied. The consequent size, mass, gonad volume and gamete production helped to track the carrying capacity of the population levels.

116. Levitan, D.R. and S.J. Genovese. 1989. Substratum-dependent predator-prey dynamics: patch reefs as refuges from gastropod predation. *Journal of Experimental Marine Biology and Ecology* 130: 111-118.

The intensity of predation pressure by gastropod *Cassis tuberosa* (L.) upon sea urchin *Diadema antillarum* (Philippi) was investigated in relation to different substrata in St. John, US Virgin Islands. Predation was preferred on sand substratum than flat rock and piled rock habitats. The quantitative results from treatment groups suggest that *Diadema* distribution and foraging may be restricted to reef habitats by predation pressure. The risks of predation may outweigh the starvation risks.

117. McClanahan, T.R. and J.D. Kurtis. 1991. Population regulation of the rock-boring sea urchin *Echinometra mathaei* (de Blainville). *Journal of Experimental Marine Biology and Ecology* 147: 121-146.

An experiment on density manipulations was carried out to explore the population regulation of *Echinometra mathaei* under conditions of reduced predator abundance. Individuals on the high-population density reef recorded urchins with smaller gonads and gonad indices (gonad wt. body wt^{-1}), lower relative gut weights, a higher fraction of calcium carbonate in gut content, larger Aristotle's lantern indices (jaw wt. body wt^{-1}) and lower respiration rates than individuals on low-density reefs. Starving experiments in aquaria explained the responses to reduced food availability. Agonistic behaviour appeared to aid in defending burrows hence reducing predator-induced mortality but not in acquiring food resources. Thus, regulation occurs at an individual level allowing high-density populations to survive low resource ambient.

118. McClanahan, T. R. and N.A. Muthiga. 2001. The Ecology of *Echinometra*. *Edible Sea Urchins.* J. M. Lawrence. Amsterdam, Elsevier. In press.

These authors have put forward a comprehensive study on the ecology of *Echinometra*. They initially discuss the controversy of different species of *Echinometra* and their history of existence. Then, they take a look at distribution and abundance patterns of *Echinometra.* Population structure in relation to environmental and ecological factors are discussed. Reproductive biology and ecology encompass the details of spawning and reproduction and a bit on the influence of environmental factors is outlined. Different modes of feeding and gut content composition are discussed in the framework of feeding ecology. The energetics outline the composition of a sea urchin and reasons for its daily needs. Growth and longevity looks at their growth rates, ways to determine their age and allocation of resources. Pelagic larval dispersal considers several factors affecting the rate of larval dispersal. Benthic population dynamics points out reasons for the stable and predictable populations of *Echinometra* over space and time. An intricate section then reveals the community ecology and coexistence where sub-sections explain the competitive interactions with other herbivores (sea urchins, fish, and predators). The effect of herbivory and grazing followed by erosion of calcium carbonate completes the overall picture.

119. McClanahan, T.R. and E. Sala. 1997. A Mediterranean rocky-bottom ecosystem fisheries model. *Ecological Modelling* 104: 145-164.

An aggregated energy-based simulation model was developed and utilized to conduct fishing experiments under varying fishing intensity and catch selection. The model was composed of primary producers (algae), herbivores (sea urchins, vagile epifauna, and herbivorous fish), suspensivores (sessile epifauna) and carnivores (piscivores and predators of invertebrates). Simulation results suggest that fishing affects the ecosystem's ecology and the benefits of fishing yields must be outweighed against changes in the benthic ecology. The model predicts that fish depletion will result in sea urchin dominance and consequent decline in algae, epifauna, and gross and net production. Addition of sea urchins to fisheries will lead to incline in epifauna and reduction in fish yields. A look is taken at the consequences of increasing or decreasing members from each trophic level. Consequently, the value of sea urchins compared with fish is important in determining harvesting policies.

120. Moore, H.B. 1964. Ecology of Echinoids. *Physiology of Echinodermata*. R.A. Boolootian. New York, John Wiley & Sons. Pp. 73-85.

Fischer-Piette (1948) said that the optimum conditions for the well being of an organism vary with the parameter used to define well-being. This paper attempts to review parameters of "well-being" of urchins. This account has been pieced from random observations and rarely from planned studies. Parameters discussed are growth rate, abundance, age at sexual maturity, maximum size, gonad production, population density feeding and metabolism, predation, burrowing and behaviour. Responses to temperature, salinity, water movement, light, pressure and food are also discussed.

121. Ogden, N.B., J.C. Ogden and I.A. Abbott. 1989. Distribution, abundance and food of sea urchins on a leeward Hawaiian Reef. *Bulletin of Marine Science* 45, no.2: 539-549.

A study involving 9 species of sea urchins was conducted along a 180m transect on a leeward Hawaiian reef in relation to algal distribution and habitat. *Echinometra mathaei* was dominant with average density of 70.3 urchins m^{-2} at 120m from shore followed by *E. oblonga* (9.3 urchins m^{-2} at 110m) and *Tripneustes gratilla* (3.7 urchins m^{-2} at 90m). Total urchin densities reached a peak average of 73.9 urchins m^{-2} at 110m. The most abundant macroalgae included *Pterocladia sp*., *Grateloupia hawaiiana* and *Acanthophora spicifera*. Out of the 43 macroalgae and 71 microalgae recorded, 19 and 14 species respectively were found in the gut content of

70 dissected urchins. Overall, the urchins responded to algal abundance when selecting food and most depended on drift algae.

122. Russo, A.R. 1977. Water flow and the distribution and abundance of echinoids (Genus *Echinometra*) on a Hawaiian Reef. *Australian Journal of Marine Freshwater Research* 28: 693-702.

Echinometra oblonga and *E. mathaei*, rock-burrowing sedentary sea urchins live in positive association on a Hawaiian reef. *E. oblonga* prevails in rough water while *E. mathaei* prefer calm water. Their distribution and abundance is positively correlated with water flow hence detrital deposition in their burrows. Their test size also seemed to increase with increase in water flow whereby both showed no significant difference in the rate in which biomass increased.

123. Watts, R.J., M.S. Johnson and R. Black. 1990. Effects of recruitment on genetic patchiness in the urchin *Echinometra mathaei* in Western Australia. *Marine Biology* 105: 145-151.

Genetic heterogeneity observed in *Echinometra mathaei* populations was attributed to relative influences of population turnover and patchiness in recruitment. Enzyme polymorphisms were examined to test the above thought. Three populations separated by 4km intervals at Rottnest Island were studied and it was concluded that the forces causing genetic differentiation act on a local scale in a single generation. Hence, all genetic variations observed between sites are due to prerecruitment effects and the urchin’s individual history of recruitment.

ABIOTIC INFLUENCES

124. Russ, G.R. and L.J. McCook. 1999. Potential effects of a cyclone on benthic algal production and yield to grazers on coral reefs across the central Great Barrier Reef. *Journal of Experimental Marine Biology and Ecology* 235, no.2: 237-254.

Reef zones, inshore (~ 10km from the coast), mid-shelf (~ 50km from the coast) and outer-shelf (~ 100km from the coast) were compared for production rates of epilithic algal community (EAC) and rates of yield to large herbivorous grazers before and after cyclone Winifred on the Central Great Barrier Reef. Inshore rates of production of EAC and yield to grazers increased by a factor of five between February 1985 and February 1986. The levels then became equitable to the nutrient concentrations on the other zones. The increase in the carbon/nitrogen ratio was noticed which resulted due to river runoffs and mineralized organic nitrogen from inshore both due to cyclone hence increasing the nutrient input to the reef. This study can be used as a guideline for the interpretation and management of cross-shelf differences in reef benthos.

125. Tsuchiya, M., K. Yanagiya and M. Nishihira. 1987. Mass mortality of the sea

urchin *Echinometra mathaei* (de Blainville) caused by high water temperature on the reef flats in Okinawa, Japan. *Galaxea* 6: 375-385.

Echinometra mathaei experienced mass mortality on the reef flats of Okinawa, Japan as a result of lethal temperatures (about 40^0C) and unusually fine weather during the day time spring low tides in June. Urchins from shallow rock pools and reef crest experienced high mortality while the ones in deeper areas of the moat and in burrows escaped the damage. The impact this event had on the intertidal community structure is discussed.

RECRUITMENT

126. Bak, R.P.M. 1985. Recruitment patterns and mass mortalities in the sea urchin *Diadema antillarum*. *Proceedings of the Fifth International Coral Reef Congress,* Tahiti 5: 267-272.

Recruitment patterns of *Diadema antillarum* (less than or equal to 3mm) was studied *in situ* on the reefs of Curacao for three consecutive years, 1982, 1983 and 1984. Spatial and temporal variation was observed between reefs. Reefs 24km apart depicted very different pictures where one showed continually higher numbers of recruits and other a lower abundance. Cleaner substrate attracted more larvae than fouled surfaces. The pattern of recruitment was consistent through time i.e. two pronounced peaks (Mar/Apr, Sept/Oct) and two less distinct (Jun/Jul, Dec/Jan) settlement peaks are observed. The urchin numbers recovered after the catastrophic mortalities within 5-6 months but were subsequently reduced to approximately zero. It is suggested that this sequence reflects the spread of mass mortalities to up-current islands and the depletion of the pool of pelagic larvae.

127. Birkeland, C. and R.H. Randall. 1981. Facilitation of coral recruitment by echinoid excavations. *Proceedings of The Fourth International Coral Reef Symposium*, Manila 1: 695-698.

A study in northern Taiwan demonstrated excavated surfaces by echinoid a good substrate for coral planulae settlement. The urchin activity facilitates coral recruitment in cracks, grooves and overhangs. A trend has been observed along a tropical-temperate gradient whereby the decrease in herbivorous fish reflects incline in fleshy algae hence successful larval recruitment becomes dependent on topographic complexity. The experiment reveals the rate at which the planulae settle in urchin grooves and flourish in them.

128. Karlson, R.H. and D.R. Levitan. 1990. Recruitment-limitation in open populations of *Diadema antillarum*: an evaluation. *Oecologia* 82: 40-44.

Empirical studies of *Diadema antillarum* suggest that this organism widely disperses its offsprings, its recruitment and mortality rates are independent of local densities and the local food availability does not regulate its local population size. Hence, these attributes imply that populations are generally open and recruitment-limited. Under assumptions of recruitment-limitation and density-independent rates of recruitment and mortality, current trends and future predictions of *D. antillarum* populations were investigated in response to the mass mortality experienced in 1983-1984. Particularly, the dynamics of 5 populations of *D. antillarum* at Lameshur Bay, St. John, U.S.V.I. were studied to (1) determine current rates of recruitment and mortality, (2) predict population densities based on above assumptions, (3) compare predicted densities against observed 1984-1988 and (4) predict future densities based on current trends. This description of dynamics of open recruitment-limited populations could apply to a variety of organisms.

129. Keesing, J.K., C.M. Cartwright and K.C. Hall. 1993. Measuring settlement intensity of echinoderms on coral reefs. *Marine Biology* 117: 399-407.

A pilot study was conducted at Davies Reef on the Central Great Barrier Reef for a month in an attempt to monitor the spatial and temporal variation in settlement rates and dispersal patterns of echinoderms via collector deployment method. This was done during summer when many echinoderms are known to spawn. Echinoids and ophuiroides were most abundant settlers while asteroids and crinoids were less common. The abundance of each class was correlated with their abundance on the natural substratum. Significant spatial variability was found in settlement rates of echinoids over 1000s of meters and ophiuroids over 100s but not over a smaller spatial scale. Difficulty was encountered in distinguishing the early echinoid settlers.

130. Schuhmacher, H. 1974. On the conditions accompanying the first settlement of corals on artificial reefs with special reference to the influence of grazing sea urchins (Eilat, Red Sea). *Proceedings of the Second International Coral Reef Symposium,* Brisbane 1: 257-267.

In situ studies were performed on harbour moles at Eilat (Gulf of Aqaba) on the initial steps of formation of coral reefs. Measurements of coral species types, their distribution, growth rates and physical parameters were recorded. More importantly, the influence of sea urchin grazing on the settlement of corals was monitored. The experimental study revealed that sea urchins considerably hindered the settlement of corals thereby restraining coral distribution to places inaccessible to urchins.

PHYLOGEOGRAPHY/TAXONOMY

131. Lessios, H.A., B.D. Keesing, D.R. Robertson and G. Paulay. 1999. Phylogeography of the pantropical sea urchin *Eucidaris* in relation to land barriers and ocean currents. *Evolution* 53, no.3: 806-817.

Four allopatric species have been recognized within the pantropical genus *Eucidaris*, *E. metularia* in the Indo-West Pacific, *E. thouarsi* in the eastern Pacific, *E. tribuloides* in both the western and eastern Atlantic, and *E. clavata* at the central Atlantic islands of Ascension and St. Helena. Gene sequencing of mitochondrial DNA was utilized to determine the division of species and to reconstruct the history of possible dispersal that may have led to current distributions. All the events that led to divergence and separation are described in the account. The phylogeny of *Eucidaris* confirms Ernst Mayr's conclusions that major barriers to the dispersal of tropical echinoids have been the wide stretch of deep water between central and eastern Pacific, the cold water southwest coast of Africa, and the Isthmus of Panama. It also suggests that a colonization event in the eastern Pacific has led to speciation between mainland and island populations.

132. Matsuoka, N. and T. Hatanaka. 1991. Molecular evidence for the existence of four sibling species within the Sea-Urchin, *Echinometra mathaei* in Japanese waters and their evolutionary relationships. *Zoological Science* 8: 121-133.

Enzyme electrophoresis was used to explore the taxonomic, genetic and evolutionary relationships of the four sibling species of *Echinometra mathaei* on the Okinawan reef flats, southern Japan. They were told apart on the basis of colour pattern of spines. The Types A, B, C and D share separate genetic plans despite their sympatric distribution, hence are reproductively isolated. Calculation of the Nei's genetic distances showed a higher difference between the four types than between the conspecific local populations. The molecular phylogenetic tree based on the Nei's genetic distances revealed close affinities between Types A and C and B and D with a large genetic differentiation between A and B. This tree also suggested relatively recent speciation during the geological age of the middle Pleistocene.

133. McCartney, M.A., G. Keller and H.A. Lessios. 2000. Dispersal barriers in tropical oceans and speciation in Atlantic and eastern Pacific sea urchins of the genus *Echinometra*. *Molecular Biology* 9: 1391-1400.

Echinometra species of the Indo-West Pacific (IWP) have been made famous through studies of phylogeny, speciation and genetic explorations. The 630 bp of cytochrome oxidase I (COI) mitochondrial gene was sequenced to provide comparable information on the eastern and Atlantic species. Most recently (1.27 – 1.62 Mya), the Atlantic species *E. lucunter and E. viridis* diverged from each other, at a time in the Pleistocene when sea levels fell and Caribbean coral speciation and extinction rates were high. An earlier split, assumed to have been coincident with the completion of the Isthmus of Panama, separated the eastern Pacific *E. vanbrunti* from the Atlantic common ancestor. The most ancient split in *Echinometra* occurred between the IWP and the neotropical clades, due to cessation of larval exchange around South Africa or across the Eastern Pacific Barrier. While gene flow was high among species, *E. lucunter* populations from the Caribbean faced restrictions on genetic exchange with species from the rest of the Atlantic. A correlation between cladogenic and vicariant events suggests that marine species form by means of geographical separation despite their high dispersal potential.

134. Negretti, B., M. Philippe, H.J. Soudet, B.A. Thomassin, and G. Oggiano. 1990. *Echinometra miocenica* Loriol, Echinide mioce’ne, synonyme *D’Echinometra mathaei* (Blainville), actuel: Bioge’ographie et Pale’oe’cologie. *Geobios* 23, no.4: 445-459.

A look at fossil evidence of *Echinometra miocenica* Loriol 1902 provides proof that it’s the modern day *E. mathaei*. A comparative list of criteria was researched to show a perfect similitude. The synonymy of both species was established on: similar pore number on each major plate, same disposition and proportion of the ambulacral and interambulacral zones, same number and places of tubercules, and similar general shape and size. Consequently, *E. mathaei* lived 16.8-17 mya, Upper Burdigalian to Lower Langhian, in the Western and Eastern Mediterranean Sea (the Red Sea being at that time a part of it). Its ecology than was probably similar to what it is now i.e. behaviour of a tropical species, eurythermal, colonizing infralittoral levels, with a cryptic or/and borer habitat on hard substrates and commonly associated with coral reefal formations. A hypothesis is proposed explaining the reoccurrence of ‘fossil-modern’ *Echinometra* species.

135.Palumbi, S.R. and E. Metz. 1991. Strong reproductive isolation between closely related tropical sea urchins (genus *Echinometra*). *Molecular Biological Evolution* 8: 227-239.

Four independent gene pools exist for the sea urchin, *Echinometra mathaei*. This was confirmed by the observed 1-3% nucleotide divergence. Thus these are the most closely related species known. Results demonstrate that strong reproductive isolation can evolve by changes in egg-sperm recognition without extensive genetic divergence between species.

136. Uehara, T., M. Shingaki and K. Taira. 1986. Taxonomic studies in the sea urchin, genus *Echinometra*, from Okinawa and Hawaii. *Zoological Science* 3: 1114.

Uehara and Shingaki performed a study (1985) in Okinawa on the distinction between the four types of urchins observed in *Echinometra mathaei*. The basis of their distinction was gamete incompatibility, differences in karyotypes and morphological features. The existing urchin types were compared from Okinawa and Hawaii and some of the types from the former corresponded to other types from latter. Colour, spicule shape and number of tubercles on madreporite were the criteria of classification.