PATTERNS AND EFFECTS OF DISTURBANCE IN CARIBBEAN MACROPHYTE COMMUNITIES

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ABSTRACT

This thesis examines a number of natural and anthropogenic disturbances within marine macrophyte habitats of the Caribbean. Understanding the effects of disturbance and the patterns associated with such dynamics is fundamental to ecological studies. Dynamics of interest included: interactions between populations; interactions between life history strategies; successional regimes; and alterations of community structure including loss of trophic heterogeneity and the possibility of "alternate" states. First I explored natural physical disturbance and succession. The dominance of macroalgae in the mid-shore, between areas of seagrass, challenged "classic" succession in such communities. I therefore proposed a model that included chronic "stress" by wave energy that could lead to a reversal in the climax state. Next, I investigated the importance of other grazers (i.e. trophic heterogeneity) in mediating the strength of trophic cascades (e.g. overgrazing). The enclosure experiments used suggested that different life history strategies respond differently to experimental conditions and that interference competition between specialist (conch) and generalist (urchins) grazers results in urchins switching to alternate resources and displaying lower condition. This dynamic may indirectly "buffer" the community against population expansions of urchins and overgrazing of diversity enhancing detritus. Under high nutrient enrichment, urchins maintained themselves, the trophic cascade and low diversity by switching to "expanded" autochthonous and "new" allochthonous resources. I continued to examine the effects of increasing nutrient enrichment, which correlated well with increasing human density, by examining eleven seagrass beds. The patterns of increasing consumer density and decreasing consumer diversity corresponded well to increasing enrichment and loss of autochthonous detritus. At high levels of enrichment, the community was dominated (> 90%) by stress tolerant/competitive producers (*Thalassia testudinum*) and generalist echinoids (> 98%). This again was thought possible through a subsidy to opportunistic producers. Finally, I set out to understand the nature of the proposed subsidy using stable isotopes (^{13}C, ^{15}N). The general pattern indicated phytoplankton, and associated detritus, increased with enrichment substantiated by significant shifts in $\delta^{13}C$ of consumers and sediment

organic material (SOM) to lighter carbon sources and change in the contribution of particulate organic material to SOM mixture from 7% to 44%. Although overgrazing of macrophyte dominated systems has often been linked to predator and competition release of urchins due to over-fishing, the contribution of nutrient enrichment should also be considered.

RÉSUMÉ

Cette thèse de doctorat examine un certain nombre de perturbations d'origine anthropiques au sein d'habitats marins des Caraïbes dominés par des macrophytes. Il est fondamental pour les études écologiques de comprendre les effets des perturbations ainsi que les patrons associés à de tels mécanismes. Les mécanismes d'intérêt incluent les intéractions entre populations, entre stratégies de cycle de vie, les régimes de succession ainsi que les altérations de la structure des communautés incluant la perte d'hétérogénéité trophique et la possibilité d'états "alternatifs". J'explore dans un premier temps les perturbations physiques et les successions. La dominance de macroalgues dans le médio-littoral parmi des zones de plantes marines remet en question la succession classique de telles communautés. Je propose un modèle qui inclut le "stress" chronique associé à l'énergie des vagues qui pourrait conduire à une inversion de l'état de climax. Nous penchons également sur le rôle d'autres herbivores (hétérogénéité trophique) en temps que tampons des cascades trophiques (p. ex. surconsommation par les herbivores). Les expériences d'enclos suggèrent que différentes stratégies de cycle de vie répondent différemment aux conditions expérimentales et que la compétition d'interférence entre les herbivores spécialistes (conques) et les généralistes (oursins) conduit les oursins à un balancement vers des ressource alternatives, associé à une condition générale inférieure. Cette dynamique pourrait indirectement "tamponner" la communauté contre des explosions des populations d'oursins et la surconsommation de détritus, lesquels rehaussent la diversité. Sous des conditions de fort enrichissement en nutriments les oursins ont maintenu leur population ainsi que la cascade trophique et ont également maintenu la faible diversité en changeant leur consommation vers des ressources autochtones "étendues" et des nouvelles ressources allochtones. Nous continuons d'explorer les effets de l'augmentation des nutrients, corrélée à la densité de population humaine, en examinant onze herbiers marins. L'augmentation de la densité et la diminution de la diversité de consommateurs est corrélée au taux d'enrichissement et à la perte de détritus autochtones. Aux forts niveaux d'enrichissement la communauté est dominée (> 90%) par des producteurs tolérants au stress (*Thalassa testudinum*) et des

échinoïdes généralistes (> 90%). Encore une fois ceci est probablement dû à un excès de ressources pour les herbivores opportunistes. Je me suis finalement penché sur la nature de cet excès de ressources en utilisant des isotopes stables (^{13}C, ^{15}N). Le patron général indique que le phytoplancton et les détritus qui y sont associés ont augmenté avec l'enrichissement, ce qui est soutenu par un balancement significatif du δ^{13}C des consommateurs et de la matière organique sédimentaire (MOS) vers des sources de carbone plus légères, ainsi que par un changement dans la contribution du carbone organique particulaire (COP) à la MOS de 7% à 44%. Bien que la surconsommation des systèmes dominés par les macrophytes ait souvent été reliée au relâchement de la prédation et de la compétition des oursins dûs à la surpêche, la contribution de l'enrichissement en nutrients devrait également être considérée.

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Fig 3: Percent biomass (gDW/m^2) of resources (Arcsine Square root transformed) along a gradient of increasing nutrient loading (based on δ^{15}N, see Fig. 1) at sites in Barbados, Dominican Republic and Panama (Table 1 for sites). (N=46). (A) Detritus, (B) *Syringodium*, (C) *Thalassia*, (D) Macroalgae. Quadratic fits were significant for (D) $\chi^2_{0.05, 1} = 1219$, $P < 0.0001$.

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(generalists); *Meoma ventricosa* (deposit feeders); *Pinna carnea* (suspension feeders).

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This thesis contains four chapters, each of which has been prepared for publication in peer-reviewed scientific journals. The first chapter has been submitted to Ecography, the second has been prepared for submission to Marine Ecology Progress Series, and the third has been prepared for submission to Ecology Letters, the fourth has been prepared for submission to Oecologia

This thesis represents the results of my own independent research. All four chapters have been co-authored by my thesis co-supervisors, Dr. Kevin S. McCann and Dr. Joseph B. Rasmussen, with the exception of the first chapter which has been co-authored by Dr. McCann and Dr. Frederic Guichard (Dept. of Biology, McGill University). Dr. McCann, Dr. Rasmussen, and Dr. Guichard contributed significantly to the design, execution, analysis, and presentation of the results presented herein.

CONTRIBUTIONS TO ORIGINAL KNOWLEDGE

Chapter 1

Investigations of the recolonization of disturbed areas, including the successional changes in community structure, are rare given the long time periods over which such successions often take place. The "classic" successional sequence of recolonization within Caribbean macrophytes has been questioned specifically with respect to the identification of climax species. Our observation of a dominant complex of macroalgae (i.e. *Avrainvillea* spp.) in the mid-shore zone of a heavily wave disturbed area, in association with near and off-shore dominated seagrass beds (*Thalassia testudinum*, *Syringodium filiforme*), put into question the well established colonization-competition tradeoffs across the entire "classic" successional sequence. Also, the existence of many small areas of acute disturbance (i.e. blowouts) at various stages of recolonization assisted in the formulation of alternative hypotheses of succession which included equilibrium (microhabitat) and non-equilibrium (patch-dynamics) forms to explain the observed pattern. We propose a modified model of macrophyte bed development and distribution that includes the important chronic "stress" category of wave energy and the inclusion of and potential dominance by macroalgae when average wave energy imposes an elevated level of stress leading to a reversal of the expected successional sequence. This reversal allows the potential existence of an alternative climax state in such systems. To our knowledge such a drastic alternative to the "classic" natural successional sequence in Caribbean macrophyte beds, and the underlying mechanisms that may bring this about, has not been previously proposed.

Chapter 2

We tested the effects, using enclosures, of habitat (resource manipulations, nutrient loading) and herbivory on a variety of producers and consumers in an effort to examine the influence of trophic heterogeneity (i.e. trophic level diversity) and the important function such a feature may have on the cascading effects of overgrazing and nutrient loading disturbances. In general, studies of the effects of diversity have largely been limited to terrestrial grassland plants and laboratory aquatic microbial systems that may not adequately represent the full range of potential effects of diversity within natural communities. In addition, although a number of enclosure studies have previously investigated species interactions between and within the basic community sub-web we used, no study had simultaneously examined a multi-species/multi-trophic configuration that may more closely resemble "real" community structure. Therefore, this study may have more clearly elucidated the important effects of diversity and the inherent variation in life history strategies in novel system (i.e. Caribbean seagrass beds). Such effects may only be perceived when ecologically significant community sub-webs representing extreme variations in life history strategies are examined in isolation. We illustrated how various life history strategies (e.g. generalists vs. specialists) respond quite differently to environmental conditions and that as chronic disturbance continues very narrow groups of organisms may remain, most notable the dominance by generalist urchins. We have also illustrated interference competition between conch (specialist) and urchins (generalist) and the resulting switch of urchins to alternate resources in the presence of superior competitors and preferred resources (i.e. detritus). This dynamic has previously been undocumented and may buffer against a release of urchin populations leading to destructive overgrazing of detritus and living seagrass, and the associated loss of diversity in Caribbean seagrass communities that have been documented in a number macrophyte communities globally.

Chapter 3

With the significant increases of allochthonous nutrient enrichment globally catastrophic changes have resulted within the food web structure of aquatic ecosystems. Such changes have been associated with the loss of species and ecosystems services, and may in fact lead to alternate states. However, little empirical work has been done to examine food webs of similar systems across a continuous gradient of nutrient enrichment. In this study, which we believe to be the first of its kind, we positioned eleven seagrass beds in Barbados, Dominican

Republic and Panama along a gradient of relatively increasing nutrient enrichment using the relationship between human population density and the stable isotope, $\delta^{15}N$, in tissues of common benthic consumers. The resulting patterns of increasing consumer density, particularly generalist urchins, and decreasing consumer diversity corresponded well to the loss of autochthonous pools of detritus. Although overgrazing of macrophyte dominated systems (e.g. California, Mediterranean, Eastern Canada) has largely been attributed to predator and competition release of urchins due to other anthropogenic disturbances (i.e. overfishing) the contribution and potential significance of nutrient enrichment is clearly highlighted here. The importance and utility of including donor-controlled alternate resources and pathways, including autochthonous detrital and other allochthonous inputs, as well as chronic forms of disturbance into food web dynamics is also stressed.

Chapter 4

In an attempt to isolate the source(s) of the suspected allochthonous subsidy to dominate generalist urchins (Chapter 2, 3) within an anthropogeniclly disturbed (urbanized, nutrient enriched) tropical seagrass food web stable isotopes were used to compare this system to a relatively unaffected (remote wilderness, control) one. Although, several other studies have alluded to the use of alternative autochthonous and allochthonous resources by urchins very few if any have done so in light of detailed community structure (i.e. Chapter 3) and producer/consumer dynamics (i.e. Chapter 2) as well as in depth stable isotope data on resources, consumers and their respective diets as described in Chapter 4. The exact nature of the subsidy is debatable, however, we present a number of feasible solutions, all directly linked to the increases in allochthonous sources of nutrients. These include elevated levels of seagrass epiphytes (actual species composition may change) and increased production and palatability (i.e. lower C:N ratios) of *Thalassia* seagrass. However, the addition of newly available phytoplankton detritus is perhaps the best supported, may best explain the dominance by generalist urchins and associated simplified community and is a novel and important finding.

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"The process of scientific discovery is, in effect, a continual flight of wonder."

Albert Einstein

This thesis is dedicated to the memory of my father,
SABRY TEWFIK
1935-2004

"Zwei Seelen wohnen in meiner Brust" from Johann Wolfgang von Goethe's Faust, 1808

.....as they do in mine.

GENERAL INTRODUCTION

The interface of disturbance, succession and life history strategies

Ecology is the study of dynamic interactions between organisms and the physical environment. Within all natural systems dynamics must include growth, death, and replacement of organisms. However, in most of these same systems a number of other factors may contribute to dynamics, with disturbance being perhaps the most significant (Dayton 1971, Pickett and White 1985). In the most general sense disturbance may be defined as an interruption or interference that alters the arrangement of the system from the "average" or "normal" conditions. Furthermore, a disturbance may be a discrete killing, damaging, or displacement of individuals that directly or indirectly creates opportunities for new individuals to become established (Sousa 1984).

However, given the extensive variety of natural disturbance regimes (e.g. fire, waves, ice storm, disease, overgrazing, predation, etc.) and the widespread spatial and temporal scale of disturbance events it may be difficult to associate them with "exceptional" or "abnormal" conditions. Although disturbance was recognized within the very earliest work by ecologists (Clements 1916), it was not part of the theory of community and ecosystem dynamics until fairly recently (Pickett and White 1985). Therefore, the understanding of the effects of disturbance and the patterns associated with such dynamics, including interactions amongst populations, successional regimes (e.g. Caribbean seagrass beds: microalgae-macroalage-*Syringodium-Thalassia*, (Patriquin 1975, Williams 1987) and changes in community structure must be considered as fundamental components of ecological studies without which no true understanding of natural systems is even likely to begin (Dayton 1971, Connell and Slatyer 1977). The general recognition of the importance of disturbance in structuring natural communities also leads to a wide ranging discussion of "alternate" or "multiple" states, that may emerge as a consequence of particular or regimes of disturbances, and the criteria that may define such alternate regimes (Sutherland 1974, Connell and Sousa 1983, Scheffer and Carpenter 2003, Knowlton 2004)

As well as being a major source of temporal and spatial heterogeneity within natural systems disturbance is also an important factor in the evolution of life history strategies (Sousa 1984). The interdependency of these two fundamental roles seems clear as we observe the variety of life history strategies that have evolved under the variety of disturbance regimes in natural systems. Therefore, life history strategies displayed by both producer (Grime 1977, Steneck and Dethier 1994) and consumer species (MacArthur and Wilson 1967, Duffy 2002) is yet another fundamental element to consider in the understanding of patterns and effects of disturbance in any natural system.

The widespread impact of disturbances resulting from anthropogenic activities (e.g. overfishing and nutrient loading) have been identified as major causes of change in the community structure of benthic marine systems (McClelland et al. 1997, Steneck 1998, Cloern 2001, Jackson et al. 2001b, Grall and Chauvaud 2002, Steneck et al. 2002, Graham 2004). These changes are thought to have begun with the extensive historic harvests of large marine vertebrate consumers and persist today with continued declines in fisheries and significant increases in nutrient loading. Continued over-harvesting (top-down) and nutrient loading (bottom-up) may work synergistically towards further species losses and trophic cascades leading to simplified food webs, homogenized landscapes, loss of ecosystem services and shifts to alternate states which may be persistent (Hughes 1994, Jackson et al. 2001b, Scheffer et al. 2001, Knowlton 2004). Again, the consideration of life history strategies represented within trophic level heterogeneity (i.e. biodiversity) of a given system is vital to understanding how communities may respond, to these "new" disturbances. The significance and utility of including donor-controlled alternate resources and pathways (e.g. autochthonous detritus, allochthonous nutrients) into food web dynamics is also carefully considered with such components possibly facilitating alternate states (Polis and Strong 1996, Huxel and McCann 1998, Polis et al. 2004).

A brief history of anthropogenic disturbance in macrophyte-dominated systems

The direct and indirect effects of anthropogenic disturbances on macrophyte-dominated coastal systems has been significant (Pearson and Rosenberg 1978, Sala et al. 1998, Pinnegar et al. 2000, Steneck et al. 2002, Nielsen 2003). California macroalgae beds (i.e. kelp forests) may serve as a typical example of such systematic overexploitation which has lead to simplified food webs. Over-harvesting began with the extinction of the mega-herbivore Stellar's sea cow in 1768 and the virtual elimination of the Southern sea otter (*Enhydra lutris nereis*) by 1911 (Riedman 1988, Estes et al. 1989). The overexploitation and subsequent declines in other competitors (e.g. abalone) and predators (e.g. lobster, sheephead) of sea urchins coincided quite well with the urchin-associated overgrazing of kelp forests in the 1950's and 1960's and subsequent explosive increases in sea urchin populations (North 1970, Tegner and Dayton 2000).

Sea urchins (i.e. *Strongylocetrotus franciscanus, S. purpuratus*) are able to maintain moderate densities even after overgrazing prohibiting the re-establishment of kelp and critical associated kelp detritus (i.e. algal drift) (Duggins 1980). The maintenance of sea urchin populations, even after overgrazing, is likely due to the great flexibility of generalist urchins to switch to alternate food resources, reduce metabolism, reabsorb tissues, assimilate dissolved organic carbon from seawater, and recruit from distant populations (Ebert 1967, Duggins 1980, Tegner and Levin 1982). The inability of the kelp canopy to re-establish prevents many formally abundant species, including the California sheephead (*Semicossyphus pulcher*), lobsters and abalone from also re-establishing (Tegner and Levin 1982, Graham 2004). Similar scenarios and mechanisms have also been described for the maintenance of high sea urchin densities in disturbed macroalgae systems of the Western Atlantic and Mediterranean (Delmas and Regis 1984, Miller 1985, Regis 1986, Sala et al. 1998, Steneck et al. 2004). Although overgrazing and deforestation of macrophyte dominated systems (e.g. California, Mediterranean, Eastern Canada) has largely been attributed to predator and competition release of urchins due to overfishing the contribution and potential significance of nutrient loading should not be ignored (Sala et al. 1998, Steneck et al. 2002) .

Seagrass-dominated systems have also undergone significant anthropogenic disturbance. These aquatic angiosperms form the basis of shallow water communities in sheltered, soft-bottom coastal areas globally contributing significantly to total production and providing a number of ecosystem services including nursery and foraging habitats, nutrient recycling, and sediment stabilization (Short and Wyllie-Echeverria 1996, Jackson 2001). In the Caribbean, *Thalassia testudinum* and *Syringodium filiforme* represent the most common basal species around which the community is structured and linked, through such processes as the export of detrius, to mangroves and coral reefs as well as pelagic and abyssal food webs (den Hartog 1971, Williams 1990).

Extensive exploitation of marine species has occurred within the Caribbean seagrass-reef-mangrove habitat complex over the last three centuries, resulting in major changes in food web structure. This began with the extensive hunting of the monk seal (*Monachus tropicalis*), now listed as extinct, and mega-herbivores of seagrasses including the West Indian manatee (*Trichechus manatus*) and green sea turtles (*Chelonia mydas*) (Jackson 1997, Timm et al. 1997, Jackson et al. 2001b).

During the last 50 years, the Caribbean has continued to be extensively over-fished with removals of large predators such as sharks, rays, groupers and snappers; intermediate predators (triggerfish and large wrasses); and herbivorous species (parrotfishes and surgeonfishes) (Koslow et al. 1988, Russ 1989, Hughes 1994). Fishing pressure has also been extensive on a number of invertebrate consumers including lobsters (i.e *Panulirus spp*), conchs (i.e. *Strombus gigas*) and sea cucumbers (holothuroidea) as well as predatory gastropods such as helmets (*Cassis spp.*) and the triton's trumpet (*Charonia variegates*) (Keller 1983, McClanahan 1999, Cochrane and Chakalall 2001, Theile 2001, Guzman and Guevara 2002).

Most recently, increases in human populations and associated urbanization within protected coastal lagoons and inadequate levels of urban sewage treatment have caused significant negative changes due to nutrient loading in these systems

(Duarte 1995, McGlathery 1995, Short and Wyllie-Echeverria 1996, Siung-Chang 1997, Jackson 2001). Again, synergistic effects of nutrient loading and over-harvesting disturbances may be expected (Hughes 1994, Jackson 2001, Thacker et al. 2001, Western 2001).

It is important to note that during this period of continued overexploitation and increased nutrient loading in the Caribbean region, generalist herbivorous urchins, notably *Lytechinus variegatus*, have been observed extensively grazing living seagrass (Camp et al. 1973, Valentine and Heck 1991, Greenway 1995, Macia and Lirman 1999). Although destructive overgrazing seems rare at present, the negative impact of such activity has been documented with the almost complete loss of the seagrass structural framework both above and below ground (Camp et al. 1973, Macia and Lirman 1999, Rose et al. 1999, Peterson et al. 2002). Such widespread changes would likely make areas formerly dominated by seagrass quite unsuitable to most traditional species.

Thesis purpose and objectives

The overall purpose of this thesis is to gain a more comprehensive understanding of the effects of a number of natural (i.e. hydrodynamics, grazing) and anthropogenic (i.e. over-fishing, nutrient loading) forms of disturbance on the community structure of Caribbean macrophyte-dominated systems. Although the absolute partitioning of specific disturbance regimes is often difficult in the field, with synergistic effects possible, the studies presented here make a best effort to do so. These systems are relatively poorly studied when compared to their temperate analogues despite containing an important pool of regional biodiversity, facilitating a number of critical ecosystem services and providing, directly or indirectly, significant sources of invertebrate and fish protein to communities both locally and internationally (Short and Wyllie-Echeverria 1996, Hemminga and Duarte 2000, Jackson et al. 2001a).

This thesis has been assembled in manuscript format with four chapters, each of which has been prepared for publication in a peer-reviewed journal. Each manuscript addresses a different aspect of disturbance in structuring Caribbean macrophyte-dominated communities and seeks to illustrate the effects of such disturbance using a number of methodologies. These methodologies include: the enumeration of producer, including associated detritus, biomass and consumer abundance using belt-transects and quadrats; the construction and monitoring of in situ enclosure/exclosure experiments; and the collection of tissue samples and subsequent analysis of stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) that may reveal origins of diet, trophic structure and relative levels of nutrient enrichment (Hobson and Welch 1992, Cabana and Rasmussen 1996, Phillips 2001). The individual manuscripts, again, explore a number of disturbance regimes in seagrass communities at a number of specific geographic locations across the Caribbean (Barbados, Dominican Republic and Panama) and as such provide several case studies from which to derive specific information. However, the thesis as a whole seeks to contribute to the basic theory and understanding of community dynamics and disturbance using Caribbean macrophyte-dominated systems (Polis and Hurd 1996, Sousa 2000). This system is an especially relevant one to consider in the context of disturbance effects given the significant losses of habitat and associated biodiversity that have result due to increasing anthropogenic activities (Short and Wyllie-Echeverria 1996, Sousa 2000, Jackson and Sala 2001).

Literature Cited

Cabana, G., and J. B. Rasmussen. 1996. Comparison of aquatic food chains using nitrogen isotopes. Proceedings of the National Academy of Science of the United States of America 93:10844-10847.

Camp, D. K., S. P. Cobb, and J. F. van Breddveld. 1973. Overgrazing of grasses by a regular urchin, *Lytechinus variegatus*. Bioscience 23:37-38.

Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation. Carnegie Inst. Washington Publ. 242:1-512.

Cloern, J. E. 2001. Our evolving conceptual model of the coastal eutrophication problem. Marine Ecology Progress Series 210:223-253.

Cochrane, K., and B. Chakalall. 2001. The spiny lobster fishery in the WECAFC region - an approach to responsible fisheries management. Marine and Freshwater Research 52:1623-1631.

Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111:1119-1144.

Connell, J. H., and W. P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. American Naturalist 121:789-824.

Dayton, P. K. 1971. Competition, disturbance, and community organization: The provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 41:351-391.

Delmas, P., and M. Regis. 1984. Influence d'une pollution complexe a dominante domestique sur les populations de l'echinoide comestible *Paracentrotus lividis* (Lamark). Vie marine 6:63-72.

den Hartog, C. 1971. The dynamic aspect in the ecology of seagrass communities. Thalassia Jugoslavica 7:101-112.

Duarte, C. M. 1995. Submerged aquatic vegetation in relation to different nutrient regimes. Ophelia 41:87-112.

Duffy, J. E. 2002. Biodiversity and ecosystem function: The consumer connection. Oikos 99:201-219.

Duggins, D. O. 1980. Kelp beds and sea otters: an experimental approach. Ecology 61:447-453.

Ebert, T. A. 1967. Negative growth and longevity in purple sea urchin *Strongylocentrotus purpuratus* (Stimpson). Science 157:557-558.

Estes, J. A., D. O. Duggins, and G. B. Rathbun. 1989. The ecology of extinctions in Kelp forest communities. Conservation Biology 3:252-264.

Graham, M. 2004. Effects of local deforestation on the diversity and structure of Southern California Giant kelp forest food webs. Ecosystems 7:341-357.

Grall, J., and L. Chauvaud. 2002. Marine eutrophication and benthos: the need for new approaches and concepts. Global Change Biology 8:813-830.

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 56:719-736.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist 111:1169-1194.

Guzman, H. M., and C. A. Guevara. 2002. Population structure, distribution and abundance of three commercial species of sea cucumber (Echinodermata) in Panama. Caribbean Journal of Science 38:230-238.

Hemminga, M., and C. Duarte. 2000. Seagrass Ecology. Cambridge University Press, Cambridge.

Hobson, K. A., and H. E. Welch. 1992. Determination of trophic relationships within high Arctic marine food webs using 13C and 15N analysis. Marine Ecology Progress Series 84:9-18.

Hughes, T. 1994. Catastrophes, Phase shifts, and large-scale degredation of Caribbean coral reefs. Science 265:1547-1551.

Huxel, G. R., and K. S. McCann. 1998. Food web stability: The influence of trophic flows across habitats. American Naturalist 152:460-469.

Jackson, E. L., A. A. Rowden, M. J. Attrill, S. J. Bossey, and M. B. Jones. 2001a. The importance of seagrass beds as habitats for fishery species. Oceanography and Marine Biology: an Annual Review 39:269-3003.

Jackson, J. B. C. 1997. Reefs since Columbus. Coral Reefs 16:S23-S32.

Jackson, J. B. C. 2001. What was natural in the coastal oceans? Proceedings of the National Academy of Science of the United States of America 98:5411-5418.

Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. B.J., R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001b. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629-638.

Jackson, J. B. C., and E. Sala. 2001. Unnatural Oceans. Scientia Marina 65:273-281.

Keller, B. D. 1983. Coexistence of sea urchins in seagrass meadows: An experimental analysis of competition and predation. Ecology 64:1581-1598.

Knowlton, N. 2004. Multiple "stable" states and the conservation of marine ecosystems. Progress in Oceanography 60:387-396.

Koslow, J. A., F. Hanley, and R. Wicklund. 1988. Effects of fishing on reef fish communities at Pedro Bank and Port Royal Cays, Jamaica. Marine Ecology Progress Series 43:201-212.

MacArthur, R., and E. O. Wilson. 1967. The Theory of Island Biogeography. Rrinceton University Press, Princeton, New Jersey.

Macia, S., and D. Lirman. 1999. Destruction of Florida Bay seagrasses by a grazing front of sea urchins. Bulletin of Marine Science 65:593-601.

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.

McClelland, J. W., I. Valiela, and R. H. Michener. 1997. Nitrogen-stable isotope signatures in esturine food webs: A record of increasing urbanization in coastal watersheds. Limnology and Oceanography 42:930-937.

McGlathery, K. J. 1995. Nutrient and grazing influences on a subtropical seagrass community. Marine Ecology Progress Series 122:239-252.

Miller, R. J. 1985. Seaweeds, sea urchins, and lobster: A reappraisal. Canadian Journal of Fisheries and Aquatic Sciences 42:2061-2071.

Nielsen, K. 2003. Nutrient loading and consumers: Agents of change in open-coast macrophyte assemblages. Proceedings of the National Academy of Science of the United States of America 100:7660-7665.

North, W. J. P., J.S. 1970. Sea urchin population explosion in Southern California Waters. Science 167:209.

Patriquin, D. G. 1975. "Migration" of blowouts in seagrass beds at Barbados and Carriacou, West Indies, and its ecological and geological implications. Aquatic Botany 1:163-189.

Pearson, T., and R. Rosenberg. 1978. Macrobenthic successions in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology: an Annual Review 16:229-311.

Peterson, B. J., C. D. Rose, L. M. Rutten, and J. W. Fourqurean. 2002. Disturbance and recovery following catastrophic grazing: studies of successional chronosequence in a seagrass bed. Oikos 97:361-370.

Phillips, D. 2001. Mixing models in analyses of diet using stable isotopes: a critique. Oecologia 127:166-170.

Pickett, S., and P. White. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando.

Pinnegar, K. M., N. V. C. Polunin, P. Francour, F. Badalamenti, R. Chemello, M. L. Harmelin-Vivien, B. Hereu, M. Milazzo, M. Zabala, and G. D'Anna. 2000. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. Environmental Conservation 27:179-200.

Polis, G. A., and S. Hurd. 1996. Linking marine and terrestrial foodwebs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. American Naturalist 147:396-423.

Polis, G. A., M. E. Power, and G. R. Huxel. 2004. Food webs at the landscape level. The University of Chicago Press, Chicago.

Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. American Naturalist 147:813-846.

Regis, M. 1986. Microstructure adaptive des radioles de *Paracentrotus lividus* (Echinodermata: Echinoidea) en milieu eutrophise par des eaux usees. Marine Biology 90:271-277.

Riedman, M. L. E., J.A. 1988. A review of the history, distribution and foraging ecology of sea otters. Pages 4-21 *in* G. R. V. a. J. A. Estes, editor. The community ecology of sea otters. Springer-Verlag, New York.

Rose, C. D., W. C. Sharp, W. J. Kenworthy, J. H. Hunt, W. Lyons, G,, E. J. Prager, J. F. Valentine, M. O. Hall, P. E. Whitfield, and J. W. Fourqurean. 1999.

Overgrazing of a large seagrass bed by the sea urchin *Lytechinus variegatus* in Outer Florida Bay. Marine Ecology Progress Series 190:211-222.

Russ, G. R. A., A.C. 1989. Effects of intense fishing pressure on an assemblage of coral reef fishes. Marine Ecology Progress Series 56:13-27.

Sala, E., C. F. Boudouresque, and M. Harmelin-Vivien. 1998. Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. Oikos 82:425-439.

Scheffer, M., and S. Carpenter. 2003. Catostrophic regime shifts in ecosystems: linking theory to observation. Trends in Ecology and Evolution 18:648-656.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature 413:591-596.

Short, F. T., and S. Wyllie-Echeverria. 1996. Natural and human-induced disturbance of seagrasses. Environmental Conservation 23:17-27.

Siung-Chang, A. 1997. A review of marine pollution issues in the Caribbean. Environmental Geochemistry and Health 19:45-55.

Sousa, W. P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15:353-391.

Sousa, W. P. 2000. Natural disturbance and the dynamics of marine benthic communities. Pages 85-130 *in* M. D. Bertresss, S. D. Gaines, and M. E. Hay, editors. Marine Community Ecology. Sinauser Associates.

Steneck, R. S. 1998. Human influnces on coastal ecosystems: does overfishing create trophic cascades. Trends in Ecology and Evolution 13:429-430.

Steneck, R. S., and M. N. Dethier. 1994. A functional group approach to the structure of algal-dominated communities. Oikos 69:476-498.

Steneck, R. S., M. Graham, B. Bourque, D. Corbett, J. Erlandson, J. Estes, and M. Tegner. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. Environmental Conservation 29:436-459.

Steneck, R. S., J. Vavrinec, and A. V. Leland. 2004. Accelerating trophic-level dysfunction in kelp forest ecosystems of the Western North Atlantic. Ecosystems 7:323-332.

Sutherland, J. P. 1974. Multiple stable points in natural communities. American Naturalist 108:859-873.

Tegner, M. J., and P. K. Dayton. 2000. Ecosystem effects of fishing in kelp communities. ICES Journal of Marine Science 57:579-589.

Tegner, M. J., and L. A. Levin. 1982. Do sea urchins and abalones compete in California? Pages 265-271 *in* J. M. Lawrence, editor. International Echinoderms Conference. A.A. Balkema, Rotterdam, Netherlands, Tampa Bayida, Florida.

Thacker, R. W., D. W. Ginsberg, and V. J. Paul. 2001. Effects of herbivore eclusion and nutrient enrichment on coral reef macroalgae and cyanobacteria. Coral Reefs 19:318-329.

Theile, S. 2001. Queen conch fisheries and their management in the Caribbean. Technical report to the CITES Secretariat TRAFFIC Europe.

Timm, R. M., R. M. Salazar, and T. Peterson. 1997. Historical distribution of the extinct tropical seal, *Monachus tropicalis* (Carnivora: Phocidae). Conservation Biology 11:549-551.

Valentine, J. F., and K. L. Heck. 1991. The role of sea urchin herbivory 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.

Western, D. 2001. Human-modified ecosystems and future evolution. Proceedings of the National Academy of Science of the United States of America 98:5458-5465.

Williams, S. L. 1987. Competition between the seagrasses *Thalassia testudinum* and *Syringodium filiforme* in a Caribbean lagoon. Marine Ecology Progress Series 35:91-98.

Williams, S. L. 1990. Experimental studies of Caribbean seagrass bed development. Ecological Monographs 60:449-469.

Abstract

Although the phenomena of physical disturbance and successional recovery from such disturbances in structuring natural communities are well known, recent studies have begun to uncover the potential for alternate outcomes or climax states in a number of systems. In this study we examine the distribution of tropical macrophytes at a heavily wave exposed site and explore equilibrium (microhabitat) and non-equilibrium (patch-dynamics) hypotheses to explain the observed pattern. The existence of a large and distinct zone of prolific macroalgae between two zones with a relatively high abundance of seagrass challenges the classic successional regime within Caribbean macrophyte beds. Significantly smaller mean size and lower frequency of acute disturbances within the macroalgae-dominated zone, as compared to the outer, mixed macrophyte zone, appears to contradict the highly disturbed environment of classic colonizers. The dominance of macroalgae in the mid-shore zone may be enhanced by the presence of large sediment sizes that are accumulated through the effect of chronic wave stress. We propose a model of macrophyte bed development and distribution that includes the important chronic "stress" category of wave energy and the inclusion of potential dominance by macroalgae when average wave energy imposes an elevated level of stress leading to a potential reversal of the expected successional sequence.

Introduction

Physical disturbance by waves can be an important force in the formation of landscape patterns and species distributions within coastal marine systems (Dayton 1971, Short and Wyllie-Echeverria 1996). Where physical disturbances are frequent and/or intense, top-down (Rose et al. 1999, Peterson et al. 2002) and bottom up forces (Williams 1987, Nielsen 2003) may become relatively unimportant in structuring the community. Physical disturbance may kill, damage or displace individuals of a resident species, thereby providing opportunities for new species to colonize the area that would normally be inhibited by the presence or activities of resident species, ultimately "resetting" the successional clock (Sousa 1984).

Within Caribbean macrophyte beds, abiotic and biotic disturbance regimes along with a classic successional sequence have previously been described where pioneering macroalgae are generally excluded over time by competitively superior seagrasses, initially by *Halodule* and/or *Syringodium* followed by *Thalassia* (generally considered the climax species), as nutrients and light become limiting (den Hartog 1971, Patriquin 1975, Williams 1987, Davis and Fourqurean 2001). This follows the well know colonization/competition trade-offs described in plant ecology where fast growing, short-lived functional groups with greater investments in propagule production are out-competed by the slower growing, longer-lived functional groups with greater investments in physical structure as environments become less disturbed (Grime 1977, Steneck and Dethier 1994).

Despite the well-founded paradigms concerning the influence of physical disturbance and the successional sequence of recovery from such disturbances, alternate outcomes or climax state shifts are possible (Williams 1990). Such alternate climax states amongst seagrass have been considered and are well documented with the competitive "inferior" *Halodule wrightii* often replacing *Thalassia* (Robbins and Bell 2000) and *Syringodium*-dominated communities persisting in some areas (Peterson et al. 2002). However, few studies have investigated seagrass-macroalgae interactions or contemplated macroalgae, which occur much earlier in the "classic" successional sequence, as a possible alternate climax state under natural or nutrient enriched conditions (Hughes et al. 2004).

Also, despite the clear importance of acute hydrodynamic forces and associated gap formation driving patch dynamics (Patriquin 1975, Bell et al. 1999, Robbins and Bell 2000) such physical energies may equally result in chronic wave stress and changed sediment characteristics which may alter growth and interactions between resident macrophytes.

Therefore, in order to examine communities for potential alternate climax states we should consider various disturbances (e.g. hydrodynamics) as potentially having acute and chronic (i.e. stress) forms which may generate very different responses, including variation in dominance, from all functional groups subjected to the disturbance (Grime 1977, Steneck and Dethier 1994, Connell 1997). The course of succession may also vary with location of the disturbed patch and associated availability and survival of colonists, sediment characteristics, nutrients, light, and impacts of grazing (Williams 1987, Cebrian 1998, Sousa 2000).

Here we report a historical shift in dominance from seagrass to macroalgae species cover in a heavily wave-exposed, shallow-water macrophyte bed in Barbados (Patriquin 1975). We further explore equilibrium (microhabitat) and non-equilibrium (patch-dynamics) hypotheses to explain the maintenance of the observed distribution. More precisely, the *Patch-dynamic hypothesis* (Paine and Levin 1981, Pickett and White 1985) suggests that inferior competitors are dynamically maintained through a high frequency of "acute" disturbances (large, discrete, short-term events) such as those caused by severe winter storms, create bare patches, initially allowing invasion by pioneering macroalgae, but which would be subsequently replaced by more competitive seagrass species. The *Microhabitat hypothesis* postulates a process by which alternate climax communities may exist at equilibrium in relation to the intensity of "chronic" (stress) disturbance (i.e. continuous, low-level water movement), dictated by relative water depth and distance from shore. This chronic disturbance alters sediment characteristics that facilitate the re-colonization of acute disturbances by the surrounding, locally dominant macrophyte species regardless of their status in the "classical" successional sequence.

These hypotheses were examined in view of landscape distributions of major macrophyte species, frequency, location and size of acute disturbances (i.e. blow-outs), chrono-sequences of succession within acute (i.e. blowouts) disturbances and sediment distribution patterns and relationships with macrophyte cover and biomass over the landscape. These observations may be important when one considers the large losses of seagrasses and associated community structure, the extensive level of coastal development, the potential importance of other chronic disturbances such as nutrient loading, and the large scale efforts dedicated to rehabilitating seagrass habitats globally (Short and Wyllie-Echeverria 1996, McClelland and Valiela 1998).

Material & Methods

Study Site

Observations for this study were made at Bath (Fig. 1) located on the east coast of Barbados, Southeastern Caribbean, during April and May of 2003. The macrophyte beds examined lie within the lee of a semi-continuous, 100 metre wide algal and coral encrusted rocky platform approximately 200 to 300 metres from shore (Patriquin 1975, Lewis and Oxenford 1996). This barrier provides some protection from the full force of Atlantic Ocean swells. The few reef lagoons and semi-protected bays around the coast of Barbados combined with strong wave energies limits the overall extent of macrophytes, especially seagrasses, around the island (Patriquin 1975).

The inshore zone of Bath is dominated by seagrasses (*Thalassia testudinum, Syringodium filiforme*) as well as fleshy (*Avrainvillea, Caulerpa, Udeota*) and calcareous (*Halimeda, Amphiroa*) green algae (Lewis and Oxenford 1996). Bathymetry and distribution of sediments, ranging from sand to rubble, have been described as complex (Patriquin 1975). Waters over the macrophyte beds are shallow (< 2 m, mean tidal range approx. 0.7 m) but generally turbulent except during a few hours around low tide (Patriquin 1975). Average wave heights are 0.3 to 0.6 metres during high tide, breaking over the entire embayment, but can exceed one metre during winter months when the coast endures large and frequent swells.

Blowouts, crescent shaped macrophyte free depressions or gaps characteristic of acute physical disturbance, occur in all substrate types at Bath (Patriquin 1975). However, blowouts are predominant in areas of low macrophyte abundance associated with early stages of succession including the outermost regions of the bed where wave action is very intense (Patriquin 1975)

Macrophyte Biomass and Percent Cover

Eighteen, one hundred metre transects, starting from the nearshore edge of the macrophyte bed, were run out perpendicular to shore every 5 metres. Two poles planted inline on the beach were used to maintain a straight course across the bed. The transect tape was secured to the substrate at various points to prevent movement. Two snorkellers assessed the overall (5 m^2 resolution) macrophyte community while swimming into shore noting where distinct changes (transition zones) in community occurred. The macrophyte bare swash zone (between the low tide waterline and inner seagrass edge), was subsequently surveyed to correct absolute distances from shore at mean low tide.

A factorial sampling regime, based on predetermined transitions and zones from initial surveys, was used to place quadrats for a detailed assessment of the macrophyte community. Three 0.25 x 0.25 m quadrats were placed by snorkelers in each zone, one in the middle and two at one metre distance in from either transition edge. During the initial set of 9 transects all aboveground macrophyte structures were removed and placed separately into ziplocs. Seagrasses, macroalgae and associated detritus were separated, rinsed of sediment and dried for approximately 24 hours at 80^{o} C to constant weight, then weighed on an electronic balance to the nearest 0.01 g. Biomass was later expressed as grams of dry weight per square metre (gDW/m^2) and converted to percent of total biomass. During the second set of nine transects, the percent cover of all macrophytes was assessed prior to biomass being removed. A PVC pole, with 0.05 m delineations, was used to assess the water depth at the site of each quadrat. All water depths were corrected to low tide using tables established for Bridgetown, Barbados.

Sediment and associated macrophyte survey

A third set of transects were deployed at 10, 30, 50 and 70 metres along the shore to investigate the relationships between macrophyte biomass, cover and sediment composition. Quadrats were placed at 23, 63 and 103 metres (corrected for swash zone) along transects in order to coincide with the approximate centre of the previously established zones. Percent cover and biomass of all macrophytes was collected, followed by the removal of all sediment down to approximately 0.1 m in depth. Macrophyte biomass was treated as before but with rinsed sediments added to appropriate sediment samples. Sediments were dried for approximately 24 hours at 80^{o} C and separated into 3 categories using a series (Wentworth scale) of sieves (cobble, > 6.73 mm, Phi < -2; gravel, 1.52 - 6.73 mm, Phi -2 to -1; sand & silt, < 1.52 mm, Phi > -1). These groups were then weighed and converted into percentages.

Blowout size, distribution and profiles

All blowouts, encountered during transect surveys within the study area, had their position within the landscape established and were measured for width in metres. Subsequent calculations established individual (based on a generic half circle area model: width $* 0.5 \Pi r^2$) and total area of blowouts within a zone. A small subset of blowouts were randomly chosen and assessed in more detail. A transect was laid across the middle of the blowout beginning at the seaward crest and moving back. Quadrats (0.25 x 0.25 m) were positioned at 0, 1, 2, 4, and 8 m (maximum distance back did deviate slightly) and all above ground macrophytes were removed. Material from the quadrats was treated as previously described for biomass surveys.

Statistical Analyses

All statistical analyses were preformed using SYSTAT version 10.2 (SYSTAT software Inc. 2002). Normality of all data sets was confirmed with tests of skewness and kurtosis (D'Agostino and Pearson 1973). Arcsine square root transformations were performed on percent macrophyte biomass and cover values as well as percent sediment to convert binomial to nearly normal distributions (Zar 1999). Analysis of variance was performed on transformed percent data using the general linear model (GLM) component of SYSTAT where interaction models are designated and categorical variables are set manually. All post hoc multiple comparisons were performed using the Tukey test which is considered to be robust with respect to departures from underlying assumptions of multiple comparisons (Keselman 1976). Finally, linear regression analyses were performed between raw (no transformation) percent sediments (independent) and macrophyte percent cover (dependent) data.

Results

The study encompassed a total area of approximately 8000 m^2. Distances from shore were all corrected, with subsequent measures of the swash zone width, to mean low tide. Three relatively distinct vegetative zones (zone I: seagrass, zone II: macroalgae, zone III: mixed macrophytes) were established based on large-scale visual surveys along 18 transects (Fig. 2). Details of macrophyte percent cover (Fig. 3a) and biomass (Fig. 3b), collected from 56 and 164 quadrats respectively, correspond well to vegetative zones and transitions. The seagrasses *Thalassia* and *Syringodium* and the species complex of the macroalgae *Avrainvillea* (predominately *A. digitata*) constitute the vast majority of biomass and cover. Other species of macroalgae and detritus represent < 2.4% and < 1% of biomass respectively and will not be dealt with further.

Two-way analysis of variance for transformed percent cover, pooled into zones, indicate a significant interaction between macrophyte species and zone (df=4, F=54.3, $P<0.0001$). Pairwise comparisons confirm significantly ($P<0.001$) lower and higher levels of *Avrainvillea* in zones I (2.6%) and II (70.2%) (Fig. 3a). No significant differences are seen between the two seagrass species in zone I or II, however, results from zone III indicate *Syringodium* (52.1%) cover is significantly higher then either *Thalassia* (19.6%) or *Avrainvillea* (13.1%) (Fig 3a).

Similar analyses for transformed percent biomass data, pooled into zones, also show a significant interaction between macrophyte species (category) and zone (position) (df=4, F=94.6, P<0.0001). Subsequent pairwise comparisons indicate significantly (P<0.001) lower and higher levels of *Avrainvillea* in zones I (8.6%) and II (94.5%) respectively (Fig. 3b). Again, no significant differences are indicated between seagrasses in zone I or II or amongst any macrophytes in zone III (Fig 3b).

Two way analysis of variance for percent sediment data show a significant interaction between sediment type (category) and zone (position) (df=4, F=18.86, P<0.0001). Subsequent pairwise comparisons indicate significantly (P<0.001) higher levels of sand than either cobble or gravel in zones I (98.4%) and III (67.5%) (Fig. 4). No significant differences are indicated between cobble (42.1%) and sand (47.4%) in zone II with only gravel (10.4%) being significantly lower than sand (Fig. 4).

Relationships between macrophytes and underlying sediments concentrated on the groups that had previously shown strong differences in analyses of variance. In this regard *Thalassia* and *Syringodium* were grouped simply as total seagrass and the gravel sediment category was omitted given its minor contribution to overall quantity of sediment. Significant (P<0.02) positive and negative regressions occurred between cobble and *Arainvilliea* and cobble and seagrass percent cover respectively (Fig. 5a). Opposite trends occurred for comparisons of *Arainvilliea* and seagrasses with sand (Fig. 5b).

The survey of blowouts (N=50) indicates a fairly even distribution of such acute disturbance features across the three zones (Fig 6). However, the mean individual size and associated total percent coverage of blowouts is significantly different between zones (df=2, F=9.06, P<0.0005) with zone three having much larger blowouts then either zones one or two. In general, macrophyte biomass transects ("Blowout profiles") across individual blowouts (N=8) indicate that recolonization of these acute disturbances largely reflects the vegetative composition of the surrounding zone which does not necessarily conform to the "classic" successional sequence for these tropical macrophyte beds (Fig. 7). This is most clear in zone I (seagrass) where *Avrainvillea* does not appear (BO2, 3) and where seagrasses are most abundant. Within zone II (macroalgae) blowouts seagrass do appear in the more recently disturbed areas just behind the crest but older areas of disturbance are populated with significant (note difference in biomass scales) amounts of *Avrainvillea* biomass (BO4, 7, 8). The outermost zone III (mixed) shows no clear pattern either in the recolonization of older or newer areas of acute disturbance within blowouts (BO1, 5, 6). In all cases the final stages of recolonization, oldest areas at the back of the blowouts, reflect the surrounding zone and seemingly appear as miniature models of what is happening at the larger zone scale.

Discussion

It is well known that the configuration of communities and the interactions within them are intimately connected to the disturbances they undergo and the functional groups of organisms that are capable of withstanding such disturbances (Dayton 1971, Sousa 2000). The seagrass community at Bath was previously studied and described as mixed seagrass cover maintained by physical disturbances in the form of blow-outs (Patriquin 1975). Although blow-outs were still shown to be a major feature of the landscape in the present study, we observed the presence of a distinct and dense zone of fleshy macroalgae, consisting of largely a single genus (*Avrainvillea*), in the mid-shore. This historical shift in dominance begged the question as to how such a feature could be maintained given the well-known classic successional sequence. This is extenuated by the fact that significant areas of competitively "superior" seagrasses (*Thalassia* and *Syringodium*) exist in the near and offshore zones proximate to the bed of macroalgae. Our results more precisely revealed three fairly distinct vegetative zones associated with distinct sediment sizes and acute disturbance (blowouts) size and frequency. We propose several mechanisms to account for the maintenance of these zones, which include the opportunity for the existence of an alternate climax state in the form of a macroalgae dominated zone. This directly challenges the generalisation of colonisation-competition tradeoffs within such systems. Finally, we describe a modified conceptual model for the development and distribution of macrophyte beds in the context of both acute disturbance and chronic stress that is compatible with our findings and which provides a testable hypothesis in seagrass ecosystems.

The maintenance of dominance and diversity across scales

The microhabitat hypothesis - The specific biotic (propagule density, vegetative structures) and abiotic (hydrodynamics, sediment nutrients) characteristics of local habitats are known to influence patterns of dominance among seagrass species (Robbins and Bell 2000). However, macroalgae have often been described as poor competitors in seagrass ecosystems although few seagrass-macroalage interactions studies have been done (den Hartog 1971, Williams 1990, Hughes et al. 2004). Our results reveal that gradients of water depth and sediment type can strongly influence patterns of dominance involving macroalgae-seagrass interactions. The *microhabitat hypothesis* is thus thought to maintain patterns of dominance in the near-shore seagrass zone I (*Thalassia testudinum* and *Syringodium filiforme*) and the mid-shore macroalgae zone II (*Avrainvillea spp.*). Here the locally abundant macrophytes ultimately re-colonize and dominate sites of acute disturbance (i.e. blowouts). It should again be noted that the presence of the clearly *Avrianvillea spp.* dominated macroalgae zone II is in contrast to observations made more than 30 years earlier where this same area was covered exclusively by seagrasses with “dense” macroalgae occurring only further offshore (Patriquin 1975).

Sediment grain size distribution within zones is relatively specific with sand predominating (>98%) in zone I and cobble being a major component (42%) of zone II. Chronic wave stress would seem a plausible mechanism to assist in the maintenance of sediment grain size composition given the bathymetric and hydrodynamic features of this coastal landscape. We may consider the generic “dissipative” beach profile or the more tide-range specific “barred dissipative” beach profile described by coastal engineers as an appropriate description of this coast (Carter 1988, Masselink and Short 1993). Such areas are characteristic of spilling breakers over a flat beach that allow the formation of nearshore bars and troughs parallel to the shoreline. Such bathymetry may assist in the accumulation of certain sediment sizes. The preference of certain macrophytes for specific sediment grain sizes is quite evident in regression analyses. Specifically, the abilities of rhyzophitic macroalgae, such as *Avrainvillea*, to colonize unconsolidated sediments is well known (Davis and Fourqurean 2001). The lower frequency and total cover of blowouts in the macroalgae zone II, as compared to the mixed zone III, strongly suggests that *Avrainvillea* is maintained as a climax community rather than through acute disturbances and associated patch dynamics.

The re-colonization pattern observed within blow-outs specific to zone I and zone II indicate a predominance for re-colonization by the surrounding, locally dominant macrophyte species. In both cases the classic successional sequence of macroalgae (e.g. *Avrainvillea*), *Syringodium*, and *Thalassia* described in the literature (Patriquin 1975, Zieman 1976, Williams 1990) is superseded by the re-colonization abilities (vegetative growth and/or propagule density) of locally abundant species. We may evoke the "inhibition" model for these first two zones (Connell and Slatyer 1977). This model assumes that any species, including later successional species such as seagrasses, may colonize a disturbed area and that these colonists will ultimately inhibit the invasion by subsequent species and persist for a very long time.

The patch-dynamic hypothesis – Acute disturbances and resulting patch dynamics have long been shown to represent a major mechanism of coexistence (Paine and Levin 1981, Pickett and White 1985). In seagrass communities, and more specifically in the macrophyte community present at Bath, acute wave disturbances have been suggested as a mechanism explaining the maintenance of diversity in a community whose dominant is *Thalassia* (Patriquin 1975, Bell et al. 1999). However, within the macroalgae-dominated zone II described in the present study, a distinctly lower overall area (3.4%) of acute disturbance exists. The mean size of acute disturbances is also significantly smaller when compared to the mixed zone III. These results suggest a relatively decreased influence of acute disturbances in driving the dominance of macroalgae, and run counter to general models of ecological succession where pioneering species, such as the macroalgae *Avrianvillea*, should dominate the most heavily disturbed areas. In contrast, the *patch-dynamic hypothesis* is thought to dominate the formation of the mixed macrophyte assemblage in the offshore zone III, as suggested by Patriquin (1975). The limitation of chronic wave stress, due to increased water depth along with mixed sediment grain size composition (cobble-20.3%, gravel-12.2% sand-67.5%) facilitates the existence of a variety of macrophyte functional groups that may exhibit a variety of sediment preferences. The significantly larger mean size, occasionally overlapping, and total area (25.2%) of blowouts further supports the idea that the mixed community is largely driven by gaps created during acute disturbance events in the offshore zone. Blow-out profiles from the zone III again suggest the more traditional colonization/competition trade offs and patch dynamics are occurring between and amongst macroalgae and seagrasses as seen during the classic successional sequence (Patriquin 1975, Davis and Fourqurean 2001). The significantly higher percent cover of *Syringodium* in zone III is further evidence of acute disturbance predominating given its status as a secondary colonizer. Interestingly, patch dynamics is shown to play a role in the maintenance of diversity in both algae dominated and mixed macrophyte zones. In both macroalgae (zone II) and mixed macrophyte assemblages (zone III), subdominant species in terms of local cover and biomass are present in blowouts. This result is in contrast with the belief that seagrass species, and more specifically *Thalassia*, are dominant slower-growing climax species, which would predict truncated (i.e. bare sediment to *Avrainvillea*) rather than the reversed successional sequences (i.e. bare sediment-*Syringodium-Thalassia-Avrainvillea*) observed here. Our results may challenge the generalisation of colonisation-competition tradeoffs within these macrophyte assemblages.

Partitioning of the hydrodynamic disturbance regime

The maintenance of spatial patterns and of diversity in seagrass ecosystems has been explained in relation to disturbance intensity (Hemminga and Duarte 2000). However, our study shows that disturbance plays a generalized role in the maintenance of diversity, but more importantly that actual successional sequences following disturbance are driven by habitat properties and/or reinforcing mechanisms leading to alternate climax states. More precisely, our results suggest that the overall physical disturbance (i.e. wave energy) regime needs to be viewed as two sub-categories: (1) an acute form that displays itself as blowouts – saucer shaped depressions – where resident organisms are at one time ripped away leaving bare sediment; and (2) a chronic form which displays itself as a continuous, low-level hydrodynamic force generated by every wave breaking across the landscape and who's intensity is most pronounced in shallow waters over nearshore bars and progressively closer to shore. The fact that a large distinct zone of prolific macroalgae (i.e. *Avrainvillea*), where seagrass were largely confined to recently disturbed areas (blowouts), existed between two zones with a relatively high abundance of seagrass, challenged the classic successional regime and the existence of well established competition-colonization tradeoffs in these communities.

In order to integrate the observations made in this study into a more generic description of macrophyte bed development and distribution we propose modifications to the model by (Hemminga and Duarte 2000), (Fig 8i). We first add the important chronic "stress" category of physical wave energy impacts on macrophytes (Fig. 8ii). This is highlighted with a clear distinction between (1) average wave energy and (2) frequency of high amplitude fluctuations bringing wave energy above the threshold for acute disturbance formation (i.e. blowouts). Under moderate average wave energy, such acute disturbances may be initially colonized by macroalgae, as in Zone III, but revert to seagrass with ample time between disturbances (Fig. 8ii:B,C). However, when the period of time between acute disturbances is short, early colonizers such as macroalgae can form the dominant cover (Fig 8ii:A). What is important here is that dominance by macroalgae is also possible when average wave energy imposes an elevated stress level leading to a reversal of the expected successional sequence as in zone II (Fig. 8ii:D-F). These alternative hypotheses can be tested using chrono-sequences of succession within 'migrating' disturbances (Patriquin 1975, Peterson et al. 2002).

It has been clearly recognized that macroalgae form an important element within macrophyte successional dynamics regardless of there position within it (den Hartog 1971, Patriquin 1975, Williams 1990, Peterson et al. 2002). However, with the realization that macroalgae may in fact form alternate climax states, which may fundamentally change community dynamics, their inclusion in models of macrophyte distribution and development are required regardless of the exact mechanism which allows this to happen.

Conclusion

This work demonstrates that an apparently single overwhelming disturbance regime, such as wave energy, may need to be partitioned into separate elements, acute and chronic, which may themselves be complicated by interactions with various biotic (macrophytes) and abiotic (coastal bathymetry and sediment composition) elements. Such partitioning is likely to yield different mechanisms for the observed pattern of community structure over relatively small scales (10s – 100s of metres). The *microhabitat hypothesis* says that locally preferred conditions (e.g. sediment) and/or locally available colonists (through vegetative growth or high propagule density) may overwhelm any generally conceived pattern of succession. The *patch-dynamic hypothesis* follows the more widely accepted “rules” of dynamic succession with early colonizers being replaced by longer-lived ones as a result of resource competition or simple attrition. Our results provide additional information on the importance of chronic, low-level forces in structuring nearshore marine communities (Siddon and Witman 2003). Any generally conceived models of succession need to be strictly examined in light of various scales of disturbance and community structure which may change “rapidly” as evidenced by the appearance of the dense zone of *Avrainvillea spp.* in the mid-shore more than 30 years after initial observations. This long term dynamic transition will provide insights into the functioning of disturbed systems and into the sensitivity of colonization-competition tradeoffs to environmental fluctuations. The general understanding of such landscape level transitions is of great relevance for the conservation of seagrass ecosystems worldwide given the large-scale losses, coastal development, increasing chronic disturbances (e.g. nutrient loading) and the significant efforts dedicated to rehabilitating seagrass habitats globally.

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Literature Cited

Bell, S. S., B. D. Robbins, and S. L. Jensen. 1999. Gap dynamics in a seagrass landscape. Ecosystems **2**:493-504.

Carter, R. W. G. 1988. Shoreline Hydrodynamics. Pages 99-149 *in* R. W. G. Carter, editor. Coastal Environments. Academic Press, London.

Cebrian, J. D., C.M. 1998. Patterns in leaf herbivory on seagrass. Aquatic Botany **60**:67-82.

Connell, J. H. 1997. Disturbance and recovery of coral assemblages. Coral Reefs **16, Suppl.**:S101-S113.

Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist **111**:1119-1144.

D'Agostino, R. B., and E. S. Pearson. 1973. Tests of departures from normality. Empirical results for the dsitribution of b_2 and $\sqrt{b_1}$. Biometrika **60**:613-622.

Davis, B. C., and J. W. Fourqurean. 2001. Competition between the tropical alga, *Halimeda incrassata*, and the seagrass, *Thalassia testudinum.* Aquatic Botany **71**:217-232.

Dayton, P. K. 1971. Competition, disturbance, and community organization: The provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs **41**:351-391.

den Hartog, C. 1971. The dynamic aspect in the ecology of seagrass communities. Thalassia Jugoslavica **7**:101-112.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist **111**:1169-1194.

Hemminga, M., and C. Duarte. 2000. Seagrass Ecology. Cambridge University Press, Cambridge.

Hughes, A. R., K. J. Bando, L. F. Rodriguez, and S. L. Williams. 2004. Relative effects of grazers and nutrients on seagrasses: a meta-analysis approach. Marine Ecology Progress Series **282**:87-99.

Keselman, H. J. 1976. A power comparison of the Tukey multiple comparison statistic. Edu. Psychol. Meas. **36**:97-104.

Lewis, J. B., and H. A. Oxenford. 1996. A field guide to the coral reefs of Barbados. McGill University, Montreal.

Masselink, G., and A. Short. 1993. The influence of tidal range on beach morphodynamics: A conceptual model. Journal of Coastal Research **9**:785-800.

McClelland, J., and I. Valiela. 1998. Changes in food web structure under the influence of increased anthropogenic nitrogen inputs to estuaries. Marine Ecology Progress Series **168**:259-271.

Nielsen, K. 2003. Nutrient loading and consumers: Agents of change in open-coast macrophyte assemblages. Proceedings of the National Academy of Science of the United States of America **100**:7660-7665.

Paine, R., and S. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecological Monographs **51**:145-178.

Patriquin, D. G. 1975. "Migration" of blowouts in seagrass beds at Barbados and Carriacou, West Indies, and its ecological and geological implications. Aquatic Botany **1**:163-189.

Peterson, B. J., C. D. Rose, L. M. Rutten, and J. W. Fourqurean. 2002. Disturbance and recovery following catastrophic grazing: studies of successional chronosequence in a seagrass bed. Oikos **97**:361-370.

Pickett, S., and P. White. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando.

Robbins, B. D., and S. S. Bell. 2000. Dynamics of a subtidal seagrass landscape: Seasonal and annual change in relation to water depth. Ecology **81**:1193-1205.

Rose, C. D., W. C. Sharp, W. J. Kenworthy, J. H. Hunt, W. Lyons, G,, E. J. Prager, J. F. Valentine, M. O. Hall, P. E. Whitfield, and J. W. Fourqurean. 1999. Overgrazing of a large seagrass bed by the sea urchin *Lytechinus variegatus* in Outer Florida Bay. Marine Ecology Progress Series **190**:211-222.

Short, F. T., and S. Wyllie-Echeverria. 1996. Natural and human-induced disturbance of seagrasses. Environmental Conservation **23**:17-27.

Siddon, C. E., and J. D. Witman. 2003. Influence of chronic, low-level hydrodynamic forces on subtidal community structure. Marine Ecology Progress Series **261**:99-110.

Sousa, W. P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics **15**:353-391.

Sousa, W. P. 2000. Natural disturbance and the dynamics of marine benthic communities. Pages 85-130 *in* M. D. Bertresss, S. D. Gaines, and M. E. Hay, editors. Marine Community Ecology. Sinauser Associates.

Steneck, R. S., and M. N. Dethier. 1994. A functional group approach to the structure of algal-dominated communities. Oikos **69**:476-498.

Williams, S. 1987. Competition between the seagrasses *Thalassia testudinum* and *Syringodium filiforme* in a Caribbean lagoon. Marine Ecology Progress Series **35**:91-98.

Williams, S. L. 1990. Experimental studies of Caribbean seagrass bed development. Ecological Monographs **60**:449-469.

Zar, J. H. 1999. Biostatistical Analysis, 4th edition. Prentice -Hall, Inc., London.

Zieman, J. C. 1976. The ecological effects of physical damage from motor boats on turtle grass beds in southern florida. Aquatic Botany **2**:127-139.

Figures

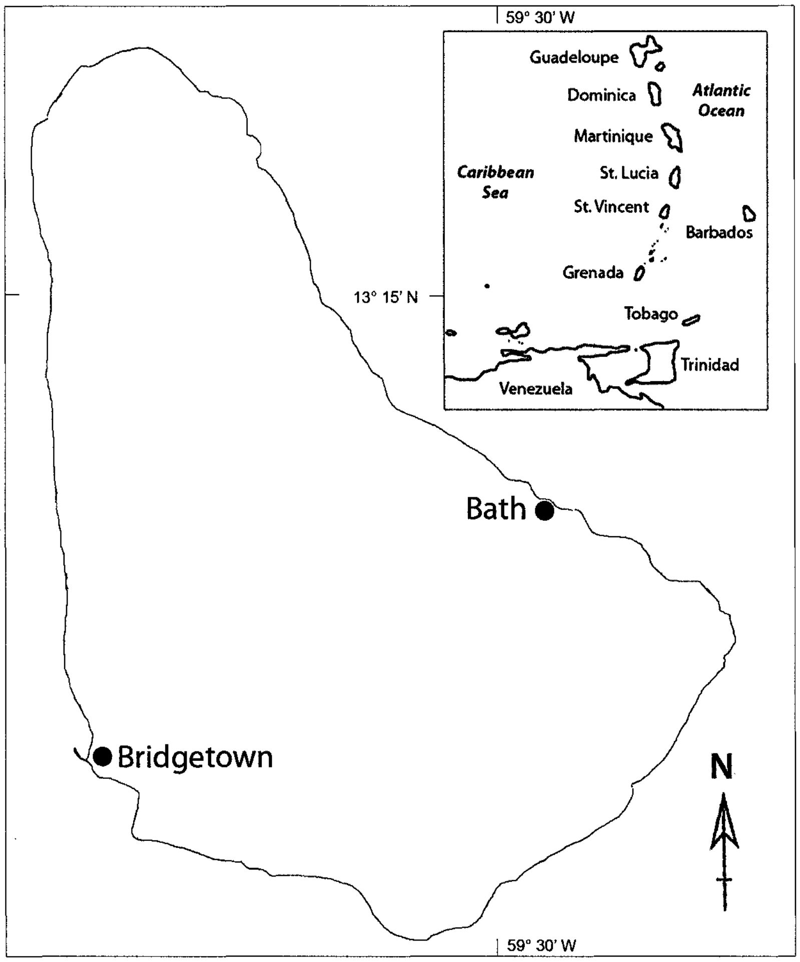


Fig. 1: Map of Barbados, West Indies including data collection site directly offshore of Bath. Inset: Location of Barbados in the Eastern Caribbean.

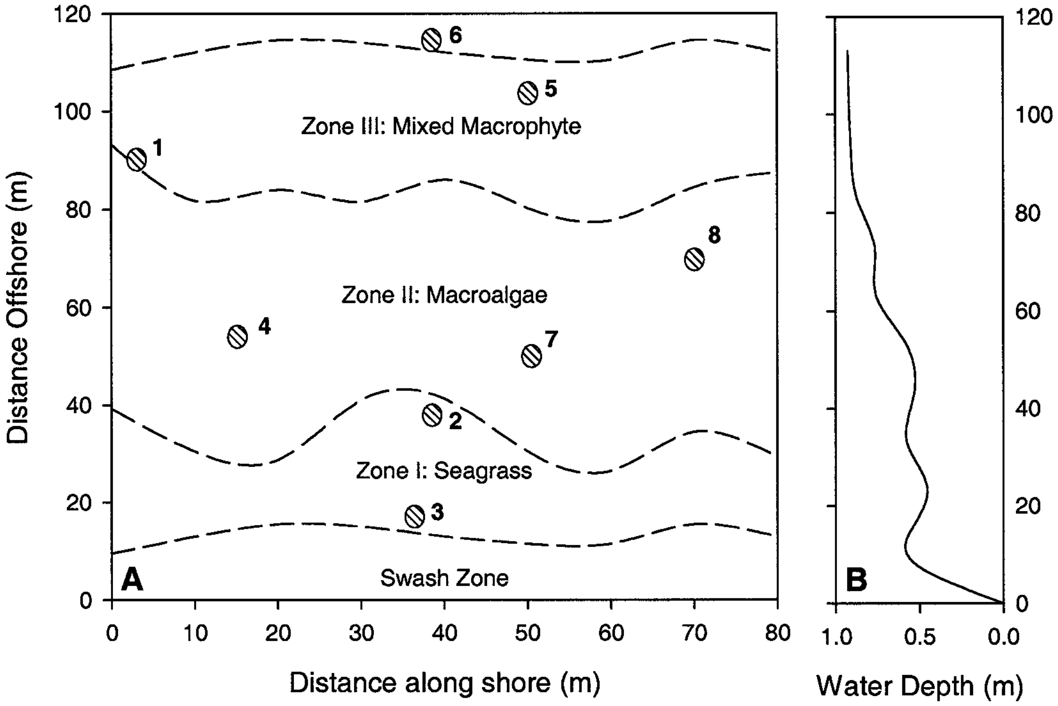


Fig. 2: Detail of study area from visual surveys at Bath, Barbados. A) Layout of vegetative zones and position of blowouts examined - profiles (hatched circles, see Fig. 7 for details). Swash zone primarily bare sand substrate with macrophytes absent, Zone I: mixed seagrass (*Syringodium*, *Thalassia*), Zone II: primarily macroalgae *Avrainvillea*, Zone III: mixed macrophytes (*Avrainvillea, Syringodium, Thalassia*). B) Mean water depth profile. All values corrected to mean low tide. Dashed lines are zone boundaries with exception of outer-most line indicating furthest extent of surveys.

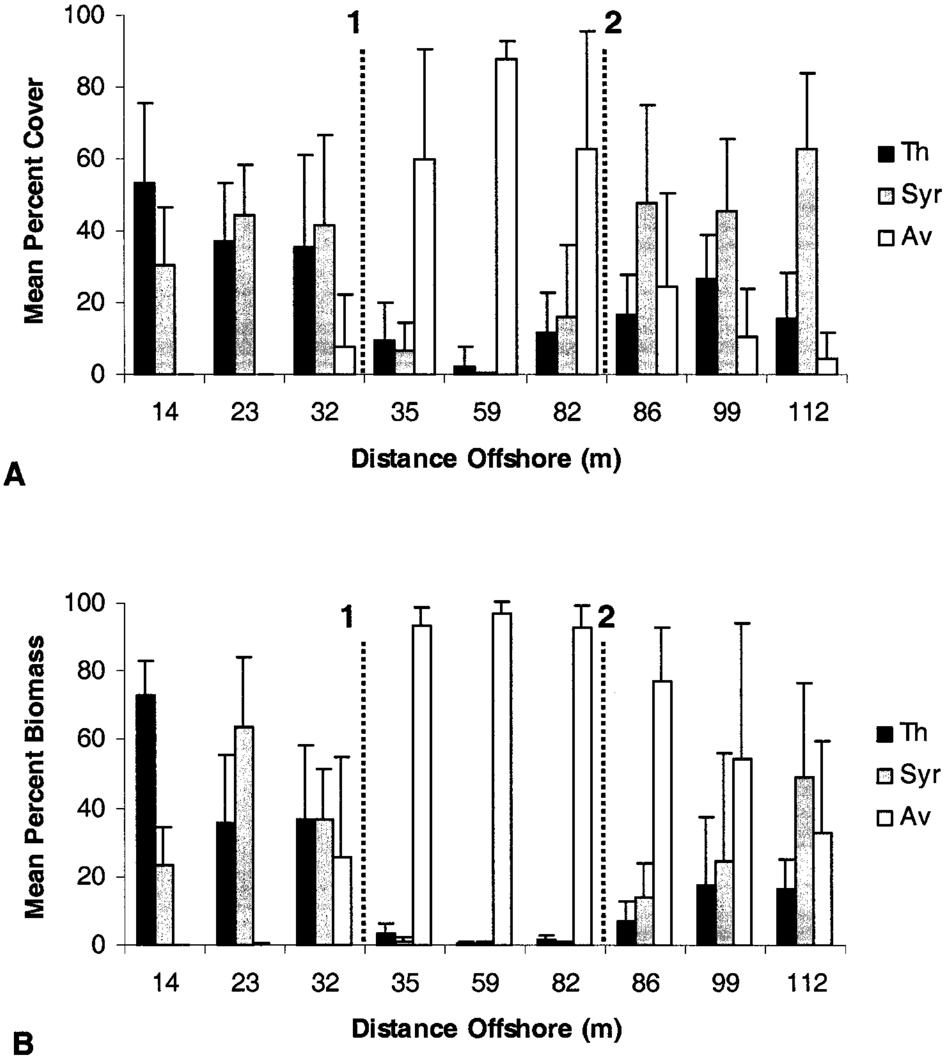


Fig. 3: Distribution of principle macrophyte species within vegetative zones. A) Mean percent cover (N=7). B) Mean percent biomass (N=18). Error bars represent one standard deviation, macrophyte species (Th = *Thalassia.*, Syr = *Syringodium.*, Av = *Avrainvillea* spp.). Dotted lines indicate approximate position of first (1) and second (2) transition (see Fig. 2). Distances corrected to swash zone.

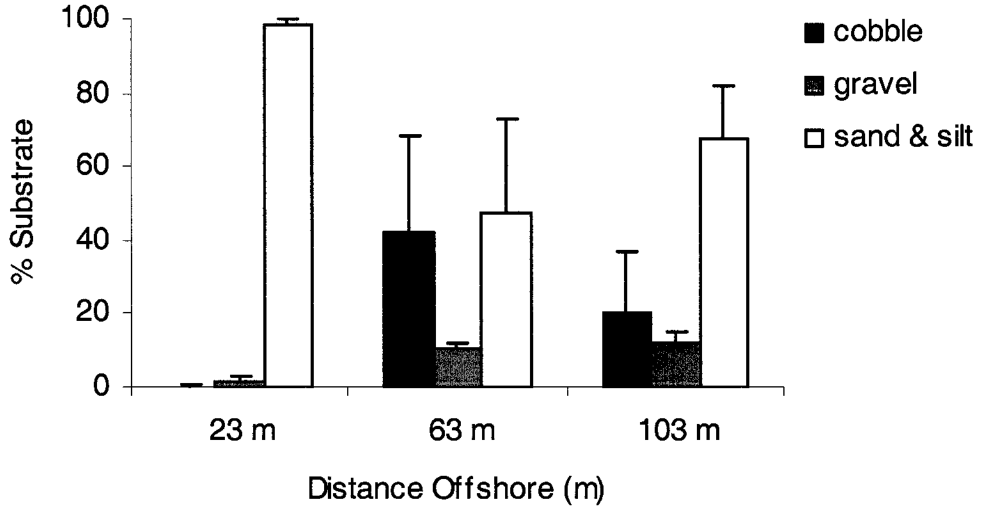


Fig 4: Mean percent sediment type within zones (see Fig 2) (N=4). Three offshore distances represent sampling at approximate centre of each main zone (see Fig. 2). Error bars represent one standard deviation.

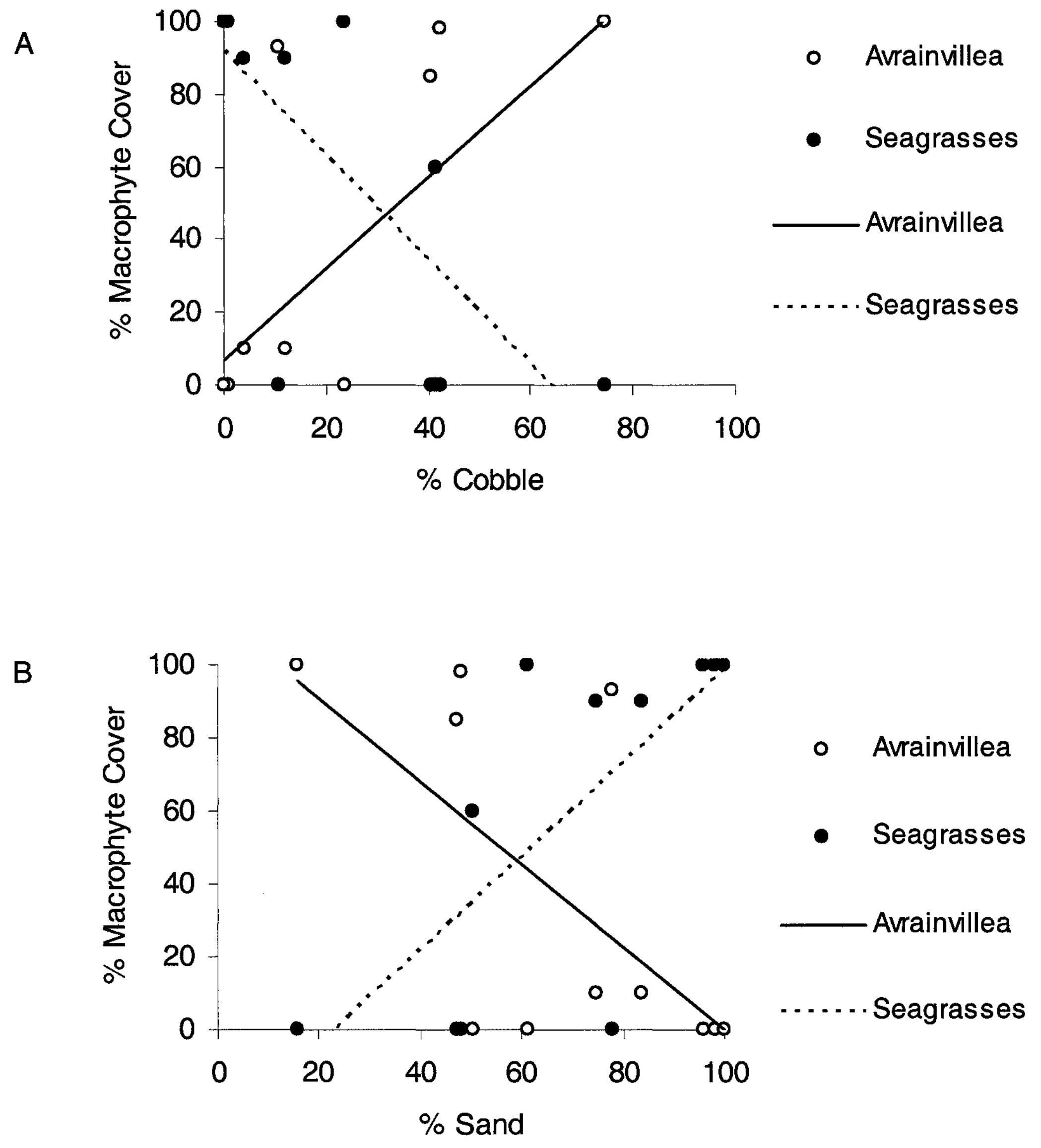


Fig 5: Relationships of substrate type (%) and macrophyte cover (%). (A) Cobble versus *Avrainvillea* spp (R^2=0.44, P=0.018) and Seagrasses (*Thalassia* & *Syringodium*) (R^2=0.54, P=0.007). (B) Sand versus *Avrainvillea* (R^2=0.45, P=0.016) and Seagrasses (*Thalassia* & *Syringodium*) (R^2=0.54, P=0.006).

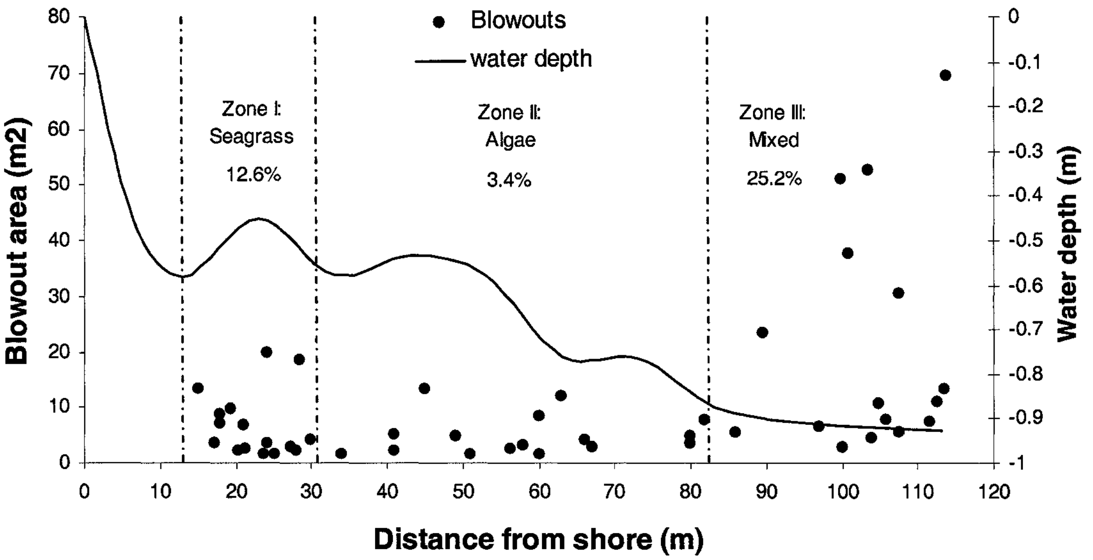


Fig. 6: Individual blow-out area (n=50), distribution and associated water depth at mean low tide. Blowout area is calculated as width * 0.5 Πr^2. Dotted lines indicate approximate position of zone transitions (see Fig. 1.2). First area is swash zone – no blowouts, percentages are total zone area covered by blowouts. Mean size of blowouts within zones is significantly different (F=9.057, df=2, P<0.0005, pairwise significant differences: zone 1 vs. 3; zone 2 vs. 3.)

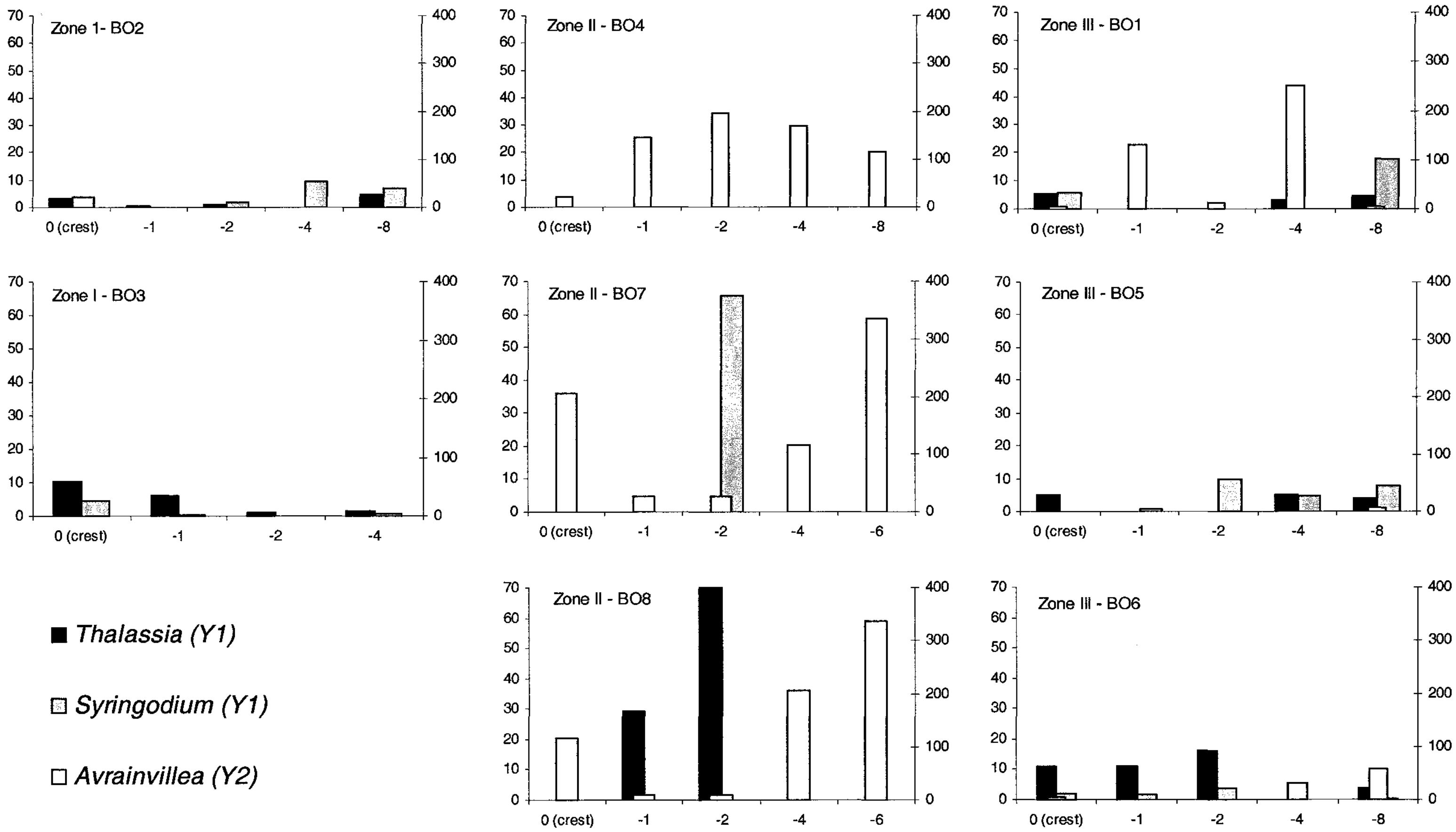
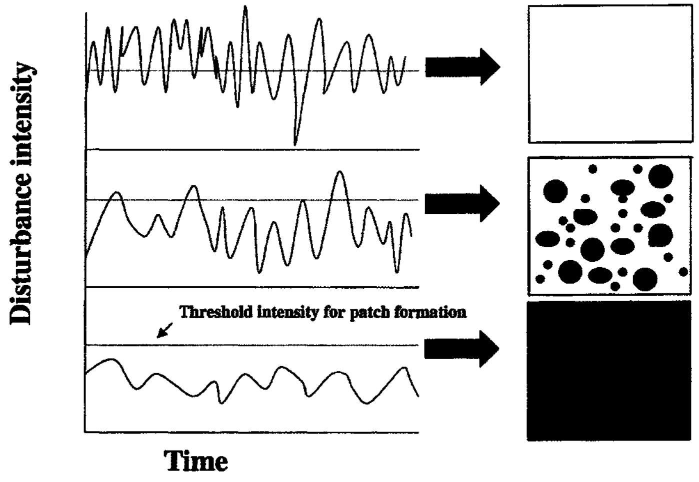


Fig. 7: Blowout (BO) profiles – biomass (gDW/m^2) of seagrass (Y1-axis) and *Avrainvillea* spp (Y2-axis) taken along transects (X-axis, in metres) within blowouts beginning at the seaward crest (0 m) and moving back. Blowout numbers refer to positions on Fig. 2.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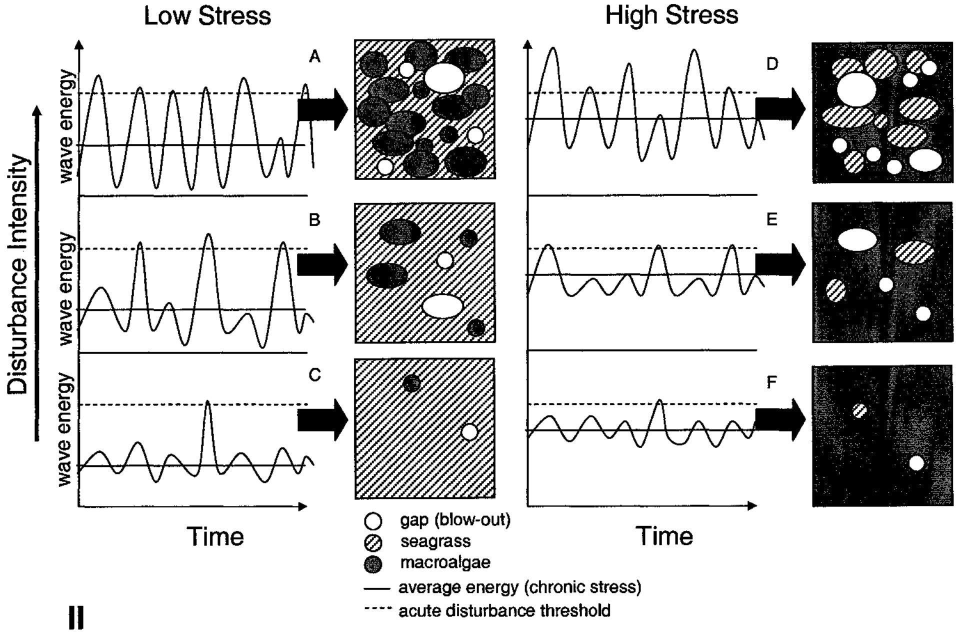
Low Stress
High Stress
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wave energy
wave energy
wave energy
A
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D
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Time
○ gap (blow-out)
▨ seagrass
● macroalgae
— average energy (chronic stress)
---- acute disturbance threshold

II

Fig. 8: Models of macrophyte bed development and distribution. i) Original model from Hemminga and Duarte 2000, Fig. 3.9, describing importance of disturbance amplitude and frequency on the development of patchy or continuous meadows, or the maintenance of bare sediments. ii) Modified model describing how chronic stress (high average wave energy, solid line) and acute disturbance (high amplitude - above threshold, dashed line) affect macrophyte dominance and patchiness within nearshore landscapes. Hatched area represents seagrass species (*Thalassia* & *Syringodium*), solid grey represents macroalgae (i.e *Avrainvillea* spp) and white represents bare areas or blowouts. Under low frequency of acute disturbance and low chronic stress seagrass dominate (C). Under higher frequencies of acute disturbance and low chronic stress seagrass remains dominant with various levels of blowouts and stages of recolonization along "classic" successional sequence (A,B). High chronic stress causes switch in dominance to stress tolerant macroalgae (F). Combinations of higher frequencies of acute disturbance and high chronic stress cause increasing frequency of bare areas and stages of recolonization with macroalgae remaining as the successional dominant (D, E).

Connecting Statement

I begin the examination of disturbance in Caribbean macrophyte-dominated systems with a relatively simple interaction between primary producers, representing colonizers and competitives, and physical of wave energy a purely natural form of disturbance, namely hydrodynamic forces (i.e. wave energy). The existence of a significant zone of macroalgae amidst seagrass dominated zones directly challenges the colonization-competition trade-offs and classic successional regimes previously documented for this specific macrophyte system and may be relevant to other important but rarely studied SG/macroalgae interactions. An important element in the understanding of the effects of such disturbances is the partitioning of the overall hydrodynamic regime into acute and chronic forms which may act very differently on alternate life history strategies within macrophytes as well as on abiotic elements such as sediments and associated nutrient levels.

In the next chapter, I continue the examination of how various life history strategies respond to disturbance. This study is much more wide ranging but controlled as it explores an important multi-trophic level sub-web of seagrass communities across a combination of habitat (i.e levels of living seagrass, detritus, nutrients) and herbivory (i.e. types and density of grazers) manipulations, using in situ enclosure experiments. The various experimental treatments attempt to replicate chronic overgrazing and nutrient enrichment disturbances. Measurements of resource biomass, consumer condition factor and resource-consumer interaction strengths confirm general predictions that stress-tolerant, generalist producers and consumers do well in chronically disturbed systems. An important element in this dominance is the loss of autochthonous detritus and associated diversity, including the specialist grazing queen conch, which may remove the "buffering" aspects of trophic heterogeneity (i.e. trophic level diversity) leaving seagrass systems vulnerable to grazing outbreaks by generalist consumers. It is suggested that a form of interference competition may represent the specific mechanism of this buffering with urchins switching to alternate resources (i.e. *Syringodium*) in the presence of the "superior" conch and abundant and preferred resources (i.e. detritus).

Abstract

Ecologists have suggested that compensatory trophic responses may be very important in governing the strength of trophic cascades in real systems. Seagrass food webs are notoriously plagued by the runaway consumptive potential of generalist grazers (i.e., sea urchins) suggesting that key compensatory grazer species may be absent. To explore the potential importance of other grazers (i.e. trophic heterogeneity) in mediating the strength of top-down control by urchins we examined a multi-species/multi-trophic sub-web containing some of the major players found in Caribbean seagrass communities, using enclosure experiments at two sites. Here, we manipulated habitat/resources and herbivory in order to address the role of trophic heterogeneity in "buffering" the cascading effects of chronic overgrazing. Specifically, we examined the generalist sea urchin *Lytechinus variegatus* and the specialist gastropod *Strombus gigas* under various levels of seagrass (*Syringodium filiforme*, *Thalassia testudinum*), detritus and nutrients as well as various levels of intra and inter-specific competition. The different life history strategies (e.g. generalist vs. specialist) represented within the sub-web responded differently to experimental conditions. The more edible seagrass, *Syringodium*, displayed decreasing biomass with increases in generalist consumers and nutrient enrichment while the less edible seagrass, *Thalassia*, appeared to be competitively released under similar conditions. Specialist *S. gigas* displayed decreased condition factor under low levels of seagrass detritus and high inter-specific competition while stress-tolerant generalists (*L. variegatus*) showed relatively unchanged condition factor until very high levels of intra-specific competition and nutrient enrichment. Our experiments also suggest interference competition with *L. variegatus* switching to alternate resources (i.e. *Syringodium*) and displaying lower body condition in the presence of *S. gigas* and preferred resources (i.e. detritus). These results suggest that the specialist *S. gigas* may play a pivotal role in mediating the dominating influence of urchins in seagrass beds. In cases without *S. gigas*, urchins appeared capable of suppressing the resource base and driving the dominance of *Thalassia*.

Introduction

In order to address the complexity of natural systems some researchers have argued for the incorporation of "trophic heterogeneity" into our examination of community structure (Hunter and Price 1992, Strong 1992). Trophic heterogeneity recognizes that different life history strategies within resource (e.g. Grime's triangle) and consumer (e.g. r-K continuum) trophic levels may play an important role in governing community dynamics (MacArthur and Wilson 1967, Grime 1977, Steneck and Dethier 1994). In particular, trophic heterogeneity recognises that horizontal trophic diversity (i.e. diversity within a trophic level) may "buffer" or "short circuit" the potential cascading effects of a major consumer through resource or interference competition, intra-guild predation or other emergent effects (Polis and Strong 1996, McCann et al. 1998, Persson 1999, Duffy 2002).

Seagrasses form the basis of shallow water communities in sheltered, soft-bottom coastal areas throughout the world (Short and Wyllie-Echeverria 1996, Duarte 2000). These communities contribute significantly to total production and provide a number of ecosystem services (Duarte 1995, Hemminga and Mateo 1996). In the Caribbean the secondary colonizer *Syringodium filiforme* and the competitive/stress-tolerant *Thalassia testudinum* represent the two most common seagrass (basal) species around which the community is structured (Randall 1965). Their distribution and relative abundance may be modified by physical forces, nutrient availability and susceptibility to herbivory (Patriquin 1975, Williams 1987, Cebrian 1998).

Two conspicuous, well-studied and strongly interactive benthic consumers within this same community are the common sea urchin *Lytechinus variegatus* and the commercially important and heavily exploited gastropod queen conch (*Strombus gigas*) (Greenway 1995, Stoner et al. 1995). The generalist, *L. variegatus*, has been known to graze detritus, epiphytes and living seagrasses and may modify seagrass beds into unvegetated barrens through destructive over-consumption (Camp et al. 1973, Valentine and Heck 1991, Greenway 1995, Macia and Lirman 1999). In contrast, *S. gigas* specialises on elements of detritus and seagrass-associated epiphytes thereby maintaining the structural integrity of the community as living seagrass and facilitating the continued existence of detrital and epiphytic pools

(Ogden 1980, Stoner and Waite 1991, Stoner et al. 1995). Detritus, in turn, is known to form important food resources and habitat for many other benthic consumers in the seagrass community as well as other systems (Stoner et al. 1995, Vetter and Dayton 1999, Moore et al. 2004). *S. gigas* may therefore be an important element of trophic heterogeneity that "buffers" or "short-circuits" a trophic cascade (i.e. overgrazing) through interference competition or intra-guild predation with *L. variegatus*, a species well known for its runaway consumptive potential (Rose et al. 1999).

In an effort to contribute to the examination of trophic heterogeneity, and its affects on trophic or ecosystem level processes (e.g. trophic cascades), a series of enclosure experiments were conducted using the aforementioned dominant basal species (*Thalassia*, *Syringodium*) and conspicuous herbivores (*Strombus gigas*, *Lytechinus variegates*), over a range of conditions. The manipulation of habitat/resources (levels of living seagrass, detritus, nutrients) and herbivory (types and density of grazers, also representing intra and inter-specific competition) conditions within enclosure treatments were prepared to create an array of overgrazing (physical cropping of resources or natural grazer effects) and nutrient enrichment (two ambient levels) levels and so provoke a variety of "responses" from tenant organisms under different conditions. Responses measured included changes in the biomass of resources, condition factor of consumers and interaction strengths between resources and consumers. The pattern of these observations would allow an evaluation of the importance of trophic heterogeneity and the associated community responses to different conditions within the significant community sub-web (see Appendix 1) examined.

Although a number of enclosure studies have previously investigated some interactions between (Stoner and Waite 1991, Valentine and Heck 1991) and within (Keller 1983, Williams 1987) trophic levels of the important community sub-web described above, no study has examined this multi-species/multi-trophic configuration concurrently include a number of the most dominate players in the real community as well as simultaneously manipulating grazers and nutrients levels (Hughes et al. 2004). Our experiments may more clearly elucidate the importance of trophic diversity and the inherent variation in life history strategies (i.e. generalist vs.

specialist) that are vital for the understanding of community dynamics and the changes that may occur under increasing levels of anthropogenic disturbances (Jackson 2001, Steneck et al. 2004). In a more general sense, studies of the effects of diversity have largely been limited to terrestrial grassland plants and laboratory aquatic microbial systems which may not adequately represent the potential effects of diversity within natural communities (Duffy 2002).

In what follows, we employ experimental enclosures to examine the following hypotheses:

(1) According to theory we hypothesize that the different consumer resources will respond to consumer density in a manner that reflects consumer preferences (Chase et al. 2002). Therefore, seagrass detritus would decrease in biomass with increasing herbivores due to its high edibility and preferred status to both consumers (Vadas et al. 1982, Stoner and Sandt 1991). *Syringodium* is also expected to decrease following the loss of detritus due to its higher edibility thus allowing the competitive release of *Thalassia* with its reduced edibility (Tribble 1981, Cebrian 1998). Increased nutrients (i.e. eutrophication) should only intensify the results above given the competitive advantage of *Thalassia* over *Syringodium* (Williams 1987, 1990).

(2) The specialist *S. gigas* (conch) should be the most influenced (e.g. decrease in condition factor) by changes in habitat and grazer density away from "pristine" conditions (i.e. high detritus and low herbivore density) while the generalist *L. variegatus* (urchins) should be relatively less influenced by such environmental changes, doing fairly well even in the most adverse conditions of low traditional resources, high herbivore density and high nutrient enrichment.

(3) According to previous suggestions of the competitive superiority in "pristine" seagrass habitats (i.e. high detritus and low herbivore density), specialist *S. gigas* should do better (i.e. higher condition factor) in mixed grazer treatments (i.e. conch + urchins) under such pristine conditions. The generalist *L. variegatus* (urchins) should thus switch resources in the wake of conch's preference for detritus even when such resources are not limiting.

If these hypotheses are correct than they together suggest two important aspects of seagrass food webs. First, under "pristine" conditions conch mediate (i.e. interference competition), in the context of a diverse primary consumer community, the consumptive potential (i.e. overgrazing) of generalist urchins. Therefore the loss or removal of conch partly allows competitive release of urchins allowing population increases that are typical of the overgrazing phenomenon. Second, the compensatory trophic responses of the seagrass *Thalassia* to changing conditions (i.e., increased nutrients and/or grazer density) and the flexibility of generalist urchins act together to reduce overall seagrass community diversity.

Material & Methods

Study Site

All enclosure experiments were conducted from February to June 2002 in the South-western Dominican Republic (Fig. 1) at a depth of 6-7 metres approximately two hundred metres from shore. The first set (Fig. 2a) of experimental treatments were set-up on the western side of the Pedernales peninsula at Baja de las Aguiles which lies within the marine boundaries of Parque Nacional Jaragua (site 1, Fig. 1). A second set (Fig. 2b) of experimental treatments were placed on the eastern side of the Pedernales peninsula within the inner harbour of the provincial capital (site 2, Fig. 1). The use of the second site at Barahona (human pop. approx. 100 000) provided the opportunity to examine a sub-set of treatments from the first experiment under the influence of extensive urbanization, including long-term nutrient enrichment, on the targeted sub-web of the seagrass community.

General ambient conditions

The general ambient conditions at the two study sites were assessed using measures of mega-invertebrate consumer densities (indiv/ha, 14 species or species groups, e.g. sea cucumbers, including *S. gigas* and *L. variegates*), diversity of mega-invertebrate fauna (Shannon-Weiner Index), resource biomass (based on gDW/m^2, including detritus, *Thalassia* and *Syringodium*), and relative levels of nutrient enrichment. Mega-invertebrate consumer densities and subsequent diversity indices were assessed along 60 x 3 metre transects (n=6 per site). The benthic resources were measured within 0.25 x 0.25 m quadrats placed at 20, 40 and 60 m along the same transect. All aboveground detritus (up to 1 cm^2) and living seagrass was removed and placed separately into whirlpacks. *Thalassia*, *Syringodium*, and detritus were then dried separately for approximately 24 hours at 80° C then weighed on an electronic balance to the nearest 0.01 g. Biomass was later expressed as grams of dry weight per square metre (gDW/m^2). The detailed methods for determination of the stable nitrogen ($\delta^{15}N$) isotopes in assessing relative levels of nutrient enrichment may be seen in (Cabana and Rasmussen 1996) and Tewfik et al., (unpublished). The stable isotope analysis for all materials was performed at the G.G. Hatch laboratories, Department of Earth Sciences, University of Ottawa. Replicate samples (N=24) showed good technical precision for $\delta^{15}N$ signals (±0.19 ‰).

Experimental Treatment Design

A two factorial design (4 x 5) was used for a number of comparisons of habitat/resources (letter codes) and herbivory (number codes) at the low (site1: Jaragua) and high (site 2: Barhona) nutrient enriched sites. Three habitat factor levels were tested at the low nutrient site: unmanipulated (seagrass and detritus: A); detritus raked out (seagrass only: B); and detritus raked and seagrass cut and removed (denuded: C), which simultaneously created three levels of resources. Seagrass at site one refers to mixed stands of *Thalassia* and *Syringodium.* The unmanipulated conditions at Barahona (site 2), *Thalassia* seagrass only and low detrital biomass in combination with extensive nutrient enrichment, represented a fourth habitat category equivalent to raked only (seagrass only) but with the addition of extensive nutrient enrichment (D). Five levels of the herbivory factor were tested: control (all mega-invertebrates removed) (1); conch monoculture (2), low density urchin monoculture (3); mixed (conch and urchin) (4); and high density urchin monoculture (5). All herbivore densities were 4 $indiv/m^2$ except for the control (0 $indiv./m^2$) and high density urchin monoculture (20 $indiv/m^2$) treatments (Fig. 2). The herbivore densities used were thought to elucidate treatment effects given results from previous experiments using the two herbivores separately (Stoner and Sandt 1991, Valentine and Heck 1991, Stoner et al. 1995, Valentine et al. 2000). The very low levels of conch at site 2 precluded the testing of conch monoculture (D2) and mixed (D4) treatments (Fig. 2a).

A second two factor experiment (2 x 4) was conceived to integrate the ambient influences of habitat/resources and herbivory at both sites and designated as open (i.e. ambient conditions) treatments (site 1: A0 and site 2: D0, see Fig. 2b). These were not fixed plots but were sampled along transects in the immediate area of the enclosures. Therefore, the second experiment consisted of two habitat levels (unmanipluted, low nutrient enrichment, A and unmanipulated, high nutrient enrichment, D) and four levels of herbivory (open, 0; control, 1; low density urchin monoculture, 3; high density urchin monoculture, 5) (Fig. 2b). All treatments, including ambient (open, 0), in both experiments included three replicates.

Enclosure Construction and Treatment Set-up

Enclosures, one meter square and 0.4 m high, were installed using SCUBA and separated by approximately three metres of ambient habitat on all sides over continuous seagrass. The enclosures were constructed from locally available materials including 0.5 cm diameter steel reinforcing bars forming the corner posts, galvanized 2.4 mm diameter wire mesh for the walls (pre-cut on land into 4.2 x 0.4 m rolls) and roof (1.2 m^2, hat box style), galvanized wire to reinforce bottom edge and plastic tie wraps to secure the mesh walls to posts (2 at each corner) and roof which was secured after habitat and herbivore manipulations were complete.

Enclosure treatment set-up, assigned randomly, involved some manipulations of the habitat/resources: raking out detritus (B, seagrass only) and cutting and raking of all seagrass and detritus (C, denuded) treatments. The nutrient enriched (elevated ambient levels at site 2) treatments (D) did not have habitat/resources manipulated although conditions were very similar to B treatments at site one with the addition of high levels of nutrient enrichment. Appropriate densities of herbivores, all juveniles of similar size within species (conch mean shell length = 138 mm, se ± 0.66: urchin mean test dia. = 44 mm, se ± 0.43) were gathered from the surrounding habitat. All other mega-invertebrate fauna were removed with exception of the open treatments (A0, D0) in the second experiment. Re-manipulation of B and C treatments were performed immediately following resource sampling approximately every 4 weeks. This was required to maintain the influence of manipulated habitats on co-occurring resources and consumers due to the natural recovery rate of seagrasses from underground structures. Dead or missing animals were replaced. The experiments ran for approximately 14 weeks (10 weeks for 20 urchin/m^2 treatments).

Resource Sampling for Grazer Effects

Resources were measured approximately every 4 weeks in a different corner of the enclosure (rotating clockwise) with a single 0.25 x 0.25 m PVC quadrat. All aboveground detritus (up to 1 cm^2) and living seagrass was removed and placed separately into whirlpacks. *Thalassia*, *Syringodium*, and detritus were then dried separately for approximately 24 hours at 80° C then weighed on an electronic balance to the nearest 0.01 gram. Biomass was later expressed as grams of dry weight per square metre (gDW/m^2) and converted to percent of total biomass.

Herbivore Condition Factor

At the end of the experiments all animals were removed from the enclosures. The physio-morphic state or "productivity" of herbivores under various treatments was assessed as a condition factor calculated as a ratio of tissue weight to a common morphometric of size. A set of animals from the immediate area surrounding the enclosures were also collected at the end of the experiments to give an "ambient" condition factor for each species. Conch were frozen for 24 hrs then thawed to facilitate complete extraction of soft tissues from the shell. Conch condition was calculated as a ratio of pat-dried wet tissue weight (±0.01 g) and shell length (±0.1 mm) (Stoner and Sandt 1991). Urchin condition was calculated as a ratio of total dry weight (± 0.01 g) (after 24hr at 80° C) and test diameter (± 0.1 mm).

Interaction strengths between resources & herbivores

Interaction strengths were calculated as the per capita interaction (Paine 1980) $(N-D)/(DY_d)$ where N = biomass of resource (gDW/m^2 at the end of experiment) with consumers present, D = biomass of resource (gDW/m^2 at the end of experiment) with consumers absent, and Y_d = density of consumers ($indiv/m^2$). These calculations were performed nine times given the combination of three replicates of producers and consumers for each treatment.

Statistical Analyses

All statistical analyses were preformed using SYSTAT version 10.2 (SYSTAT software Inc. 2002). Standard level of significance is 0.05 unless otherwise indicated. Normality of all data sets was confirmed with tests of skewness and kurtosis (D'Agostino and Pearson 1973). Paired t-tests were conducted to examine differences between ambient conditions at the two sites. These analyses were carried out using log (n+0.03) transformed data of biomass (gDW/m^2) and log (n+10) transformed data of density (indiv./ha) (n+x values reflecting appropriate minimum detection limits) for resources and primary consumers respectively and untransformed diversity data (Shannon-Weiner index).

Arcsine transformations were performed on percent resource biomass values from treatments to convert binomial to nearly normal distributions (Zar 1999). Potential problems relating to constraints in the covariance and correlation structure may be encountered when using compositional data (Jackson 1997). However, given the fact that similar patterns were observed using raw resource biomass data, with the exception of *Thalassia*, “it is of little consequence which form of data is chosen” (Jackson 1997). Therefore, only the compositional data will be presented for resources.

Analysis of variance was performed on transformed percent resources, condition factor and interactions strengths using the general linear model (GLM) component of SYSTAT where interaction models are designated and categorical variables are set manually. All post hoc multiple comparisons were performed using the Tukey test which is considered to be robust with respect to departures from underlying assumptions of multiple comparisons (Keselman 1976). Finally, linear regression analyses were performed between raw (no transformation) mean percent resources (independent) and mean condition factor (dependent) data.

Results

General ambient conditions

Overall mega-invertebrate benthic consumer densities, composed of primarily herbivores/detritivores, were siginficantly different (t=11.90, df=5, p<0.0005) largely due to the very high numbers of the sea urchin *L. variegatus* (t=-8.89, df=5, p<0.0005) at site 2 (Fig 3a). Corresponding densities of *Strombus gigas* at site 2 were recorded as zero within transects, although a few individuals were found during other work, and therefore significantly lower than at site 1 (t=15.74, df=5, p<0.0005) (fig. 3a). The diversity of mega-invertebrate fauna (Shannon-Weiner Index) was also different (t=-6.19, df=5, p=0.0016) (Fig. 3b). Standing crops (based on gDW/m^2) of detritus and *Syringodium* were both significantly higher (p<0.0005) at site one (Fig. 4). Significantly elevated (p<0.05) levels seagrass epiphytes were found at the nutrient enriched site 2. However, no such difference was found for *Thalassia* (t=0.522, df=5, p=0.62). Finally, indications of nutrient enrichment levels, based on stable nitrogen isotope ($\delta^{15}N$) values, were also very different for both resources and consumers between the two sites. Delta N^{15} values were elevated by 2.65 (t=21.25, df=3, P<0.0005), 3.02 (t=8.61, df=3, P<0.005), 3.78 (t=10.21, df=7, P<0.0001) and 4.11 (t=14.91, df=4, P<0.0002) delta units for *Thalassia*, detritus, *L. variegatus*, and *S. gigas* respectively at site 2.

Grazing and Habitat Effects

Within the first experiment all final percent biomass levels of resources were significantly affected by both habitat and herbivory and no significant interactions were apparent between the two factors (Fig. 4, Table 1a). In particular, the high urchin monocultures (A5, B5, C5) had significantly lower levels of resources in almost all treatments with urchins displaying particularly effective cropping of both detritus and *Syringodium* to very low levels (< 1.5 gDW/m2). This dramatic loss of biomass was not so apparent for *Thalassia* with standing crops ranging from 30.7 (se ± 1.8) to 38.0 (se ± 9.8) gDW/m^2 although differences in biomass were still statistically lower than other herbivore treatments (Table 1a). Significantly higher ($p=0.041$, Table 1a) levels of *Syringodium* were found in the conch monocultures (A2, B2, C2) when compared to the mixed herbivore treatments (A4, B4, C4).

Again, in the second experiment, all final percent biomass levels of resources were significantly affected by both habitat and herbivory treatments and no significant interactions were apparent between the two factors (Fig. 5, Table 1b). The clear differences between ambient resources at site 1 (A) and site 2 (D) and the strong effect of the high urchin monoculture (20/m^2, herbivore treatment, 5) on all resources, including results from the open treatments (A0, D0), were again observed (Table 1b). It is interesting to note that levels of detritus within the D habitat under this heavy herbivory (20 urchins/m^2) were significantly higher than in the other high urchin monoculture (A5, B5, C5) treatments (Detritus: $df = 3$, $F=8.61$, $p=0.01$). This is not so for *Syringodium* as it was not present at site 2.

Herbivore Condition Factor

Overall condition factor for both herbivores varied across treatments in both experiments (Fig. 5). Replacement of herbivores due to death only occurred for a single replicate of the B5 treatment mid-way through the experiment and may be due to predation by a drilling predator, possibly *Cassis* spp. Highest condition factors occurred under very different habitat conditions for conch (A0) and urchins (C3) with the lowest condition factors at C2 and D5 for conch and urchins respectively (Fig. 5). Analysis of variance revealed the significant effect of habitat on conch with pairwise difference between "pristine" (A), denuded (C) (Table 2a) and pristine and enriched (D) conditions (Table 2b). Analysis of variance also revealed a significant interaction between habitat and herbivory on condition factor for urchins (Table 2a). Significant pairwise interactions for urchins included differences between treatments of extremely high and low resources (e.g. A3 vs D3, A5 vs D5) and high and low herbivore densities (e.g. C3 vs C5). This included significantly higher condition in the

C3 denuded, low density, urchin monoculture versus the C4 denuded, mixed herbivore treatment (Table 2a). Experiment two results precluded the interactive effects of habitat and herbivory yet both factors were responsible for significant differences in urchin condition: differences between sites (A vs D habitats) and conspecific densities (low vs high and high vs ambient urchin densities) (Table 2b). Regression analyses performed between percent biomass of resources and condition factor revealed a number of significant trends (Fig. 6). Conch had an increased condition with increasing detritus (Fig. 6a) and urchins had an increased condition with increasing *Syringodium* (Fig 6c). No significant relationships occurred with *Thalassia* for either herbivore (Fig. 6b).

Interaction Strengths

These analyses were restricted to treatment configuration for experiment one (Fig. 2a) as absolute ambient (i.e. A0 and D0) herbivore densities were not known precluding the calculation of interaction strengths. No significant interactions between habitat and herbivory were observed for detritus with significant pairwise differences observed only between unmanipulated (A) and nutrient enriched (D) habitats and high (5) and low (3) urchin densities (Fig.7, Table 3). No significant results occurred for interactions involving *Thalassia*. Finally, *Syringodium* results did show a significant interaction between habitat and herbivory (Table 3). Significant pairwise comparisons included the low urchin monoculture (A3) versus the mixed herbivore (A4) treatment and conch monoculture (C2) versus low urchin (C3), mixed herbivore (C4) and high urchin (C5) treatments (Table 5).

Discussion

The structure of communities and the dynamics within them may be largely influenced by the environmental conditions and the types (life history strategies, functional groups) and variety (diversity, trophic heterogeneity) of organisms that are capable of living under those different conditions (Dayton 1971, Sousa 2000). Here, we examined how various life history strategies interacted under a combination of habitat/resource and herbivory regimes ultimately representing several forms of chronic disturbance (i.e. overgrazing and nutrient enrichment). In general, as with previous studies in seagrass beds, mega-invertebrate grazers exert a strong top-down pressure on resources (Stoner and Sandt 1991, Greenway 1995, Valentine and Heck 1999). However, the more interesting and novel results involve the different ways this top-down pressure displays itself depending on the interactions of available resources (i.e. habitat) and grazers (i.e. herbivory, competition) as well as in the context of strong bottom-up influences (i.e. nutrient enrichment).

Ambient conditions: Setting the stage

Resource levels at the open (ambient) treatments (site 1:A0, site 2: D0) most closely resembled enclosed treatments A1 (unmanipulated habitat and zero herbivores) and D5 (unmanipulated, nutrient enriched habitat and 20 urchins/m^2) at site 1 and 2 respectively and most likely reflect the overall levels of primary consumers (0.21 and 6.67 indiv./m^2) at those sites. Overall consumer density is 32 times higher at site 2 with the vast majority of elevated consumer density (98.5%) and associated low diversity (0.23) represented by the generalist consumer *L. variegatus*. In contrast, site 1 has a much higher diversity (1.48) with consumer density representing a much wider variety of consumers including *S.gigas* (22.3%) and *L. variegatus* (12.9%). In addition, site 2 has clearly elevated levels of anthropogenic-derived nutrient enrichment (based on $\delta^{15}N$ as seen in other studies, (Cabana and Rasmussen 1996, McClelland et al. 1997) entering the system from the adjacent watershed. The combination of strong and chronic top-down (high herbivory) and bottom-up (nutrient enrichment) forms of disturbance at site 2 has resulted in a simplified community at both the producer (e.g. no *Syringodium*) and primary consumer (6 times lower diversity) levels. The complete absence of *Syringodium* is likely due to a combination of high herbivory, low light and competition from *Thalassia* (Williams 1987, Cebrian 1998) resulting in the producer community being dominated by *Thalassia* (>95% biomass). The distinction between chronic and acute forms of disturbance is important in explaining the presence of the dominant forms (i.e. *Thalassia*, *L. variegatus*) and may run counter to the kinds of species that are present where more classic, acute natural disturbances occur (Sousa 2000, Siddon and Witman 2003).

Patterns of resources: Variation in palatability

As expected, clear reduction of detritus, being the preferred food source for many macro-consumers (Vadas et al. 1982, Stoner and Sandt 1991, Vizzini et al. 2002), was observed with increasing density of herbivores in a number of treatments. The abundance of *Thalassia* displayed an opposite trend, although statistical differences were limited, due partially to its competitive nature (Williams 1987) as well as the complete lack of herbivory by conch and the likely higher levels of defensive compounds (e.g. lignin) in the leaves making it less edible to the generalist urchins (Tribble 1981, Stoner et al. 1995, Cebrian 1998). It should be noted that the consumption of *Thalassia* by generalist urchins may be highly variable with respect to spatial and temporal parameters (Valentine et al. 2000, Valentine and Heck 2001). Never the less, interaction strengths show no significant effects of either herbivore on *Thalassia* again suggesting low edibility or at least tertiary preference to consumers known to use such resources (i.e. urchins) in this sub-web. The patterns of *Syringodium* abundance again suggest that the slower-growing, larger competitive *Thalassia* is more resistant than the faster growing, early colonizing, more edible *Syringodium* under increasing pressure from generalist herbivores (Cebrian 1998, Vaitilingon et al. 2003). A lower abundance of *Syringodium* was observed within the mixed herbivore treatments (A4, B4, C4) when compared to the low density urchin monocultures (A3, B3, C3). This may suggest some form of interference competition, in light of the availability of preferred detritus resources, between the two consumers. Conch, the superior competitive specialists, are expected to consume the preferred detritus while urchins may switch or be "forced" onto the living *Syringodium* as an alternative resource. This observation may be further supported by statistically significant differences in interaction strengths where *Syringodium* suffers negative interactions in the unmanipulated, mixed herbivore (A4) treatment. The observation of diversity effects such as resource partitioning or interference competition is thought to become apparent only when examining a relatively wide or representative range of species richness (Duffy et al. 2001, Duffy et al. 2003). However, such effects may also be perceived when ecologically significant community sub-webs representing strongly interactive species with extreme variations in life history strategies (i.e. generalists vs. specialists) are examined in isolation. The perception of such diversity effects may be illustrated by this study and the potentially analogous case of specialist abalone "controlling" generalist urchins in California kelp beds (Deacon 1973, Tegner and Levin 1982, Karpov et al. 2001).

Condition factor: Opposite trends and preferred habitats

It appears that the highest condition factors of our focal consumers are achieved under very different conditions. Conch appear to prefer the high detrital biomass and low consumer density (0.21/m^2) environments of ambient, "pristine" seagrass beds found at site 1 (A0 treatment) with urchins doing best in denuded habitats with moderate con-specific densities (C3 treatment). The C3 environment may provide low but highly nutritional food resources to urchins in the form of young, extremely edible shoots of *Thalassia* and *Syringodium* as these resources recover from disturbance through below ground structures. In contrast, the dense seagrass and detritus "jungle" preferred by conch may create a difficult environment for urchins to graze and move within and also harbour many other competitors (e.g. *Tripneustes ventricosus*) and predators (e.g. helmet shells – *Cassis* spp.) (Keller 1983, Greenway 1995).

Factorial analysis indicates that condition factor of urchins in our experiments is significantly determined by both resource availability (i.e. habitat factor which include nutrient levels) and competition, both intra- and inter-specific (i.e. herbivory factor). This does not appear to be so for conch where condition is determined by habitat/resource availability, best exemplified by the large change in condition from "pristine" (A) to denuded (C) habitats. However, given the significant changes in ambient conditions from site 1 (A habitat) to site 2 (D habitat), including highly elevated levels of sea urchins (6.65/m^2), the influence of inter-specific competition would be expected although this may display itself indirectly through the urchins ability to modify the habitat through resource, specifically detritus, removal. We would also expect conch to be influenced by intra-specific competition at densities or temporal scales beyond this study. At the same time, the direct effects of inter-specific competition seem to favour conch. In mixed herbivore, low resource level treatments (C4) conch and urchins had higher and lower condition factors respectively when compared to similar habitat treatments involving only intra-specific competition (i.e. C2 and C3). This may provide further evidence as to the "superior" competitive abilities of conch over urchins.

The significantly lower urchin condition in all treatments at site 2 (D0, D3, D5) when compared to site 1 indicates that some environmental conditions (e.g. chronic nutrient loading and lack of diverse traditional resource base) may create a challenge for urchin growth as mentioned earlier. However in general, observations across the wide range of resources (habitat factor) and competition (herbivory factor), both intra and inter-specific forms, treatments examined in this study suggest that *L. variegatus* is clearly a generalist with a flexible diet that is able to do reasonably well even in heavily disturbed environments (Greenway 1976, Vadas et al. 1982, Keller 1983).

The regressions involving resources and condition factor provide additional evidence on the importance of detritus to the diet of specialist conch with neither *Thalassia* (except indirectly through donor-controlled detritus) nor *Syringodium* showing significant effects. A slightly surprising result shows how *Syringodium* does have a significant positive effect on the condition of *L. variegatus* and is perhaps why site 2, where *Syringodium* is absent, shows significantly lower urchin condition. Again, *Thalassia* showed no effect on the condition of urchins.

Allochthonous inputs extend flexibility and survival

Despite the considerable flexibility of the urchin diet facilitating existence across a wide range of environments and associated disturbances it is somewhat difficult to understand how the highest populations of urchins we observed ($6.65/m^2$ ± 2.25) persisted in what appeared to be the poorest conditions (site 2: low levels of preferred resources; high intra-specific competition; high nutrient enrichment). The key to resolving this apparent dichotomy may be in the realization that the high nutrient enrichment, often considered a negative influence in nearshore marine systems (McClelland et al. 1997, Grall and Chauvaud 2002), may be the very element that allows such high densities of urchins, although of lower condition factor, to persist year after year.

The terrestrially derived, anthropogenic nutrient enrichment may subsidize urchin survival through several possible pathways. The most direct route has urchins taking up dissolved organic carbon from the water column through their water vascular system (Lawrence 1975, Regis 1986, Beddingfield and McClintock 1998). Several other pathways, involving increased levels of nutrients to primary producers include: 1) "allochthonous" resources of phytoplankton detritus (Iken et al. 2001, Polis et al. 2004), settling to the benthos from blooms of phytoplankton in the pelagic; 2) increased epiphytic growth on seagrass (McGlathery 1995) that settles to the sediment; and 3) increased growth and leaf turnover of *Thalassia*, the living grass becoming more edible due to higher nitrogen (i.e. lower C:N ratios) content (McGlathery 1995, Adams and Sterner 2000). The higher levels of detritus and unchanged levels of *Thalassia* within enclosures under heavy herbivory and nutrient loading (D5: 20 urchins/m^2) when compared to other high urchin treatments (A5, B5, C5) may indicate that dissolved carbon, increased epiphytic or phytoplankton detrital resources, or a combination, are more preferred over *Thalassia* detritus (although still consumed) and the leaves themselves in the nutrient subsidized environment. This allows an additional release of *Thalassia*, first lacking competitors (i.e. *Syringodium*) and now predators (i.e. urchins), in the nutrient rich environment (habitat D, site 2). Ultimately, the bottom-up driven subsidy (i.e. nutrient enrichment of primary producers) may allow the continued survival of urchins at elevated densities which then continue to overgraze seagrass detritus thereby maintaining the trophic cascade (top-down driven) and the simplified, low diversity community.

Conclusions

Although the exact nature of a subsidy is not completely understood in this study the presence of one may be a plausible explanation for the persistence of high densities of well defended, low edible, stress-tolerant organisms (*Thalassia* and *L. variegates*) and the associated simplified communities observed. The identification of such a subsidy is critical and is the focus of another study (Tewfik et al., unpublished). However in a more general sense, we have illustrated how various life history strategies (e.g. generalists vs. specialists) respond quite differently to environmental conditions and that as chronic disturbances continue very narrow groups of stress-tolerant organisms and low community diversity may remain.

We have also suggested the positive effect of horizontal trophic heterogeneity, specifically as predicted in our three general hypotheses, by illustrating interference competition between conch and urchins. As a result of this interaction urchins switch to alternate resources (i.e. *Syringodium*) in the presence of the "superior" conch and abundant and preferred resources (i.e. detritus). It should be noted that the superior competitive abilities of conch are likely only displayed under idealized or "pristine" (i.e. high detritus and low herbivore density) habitat conditions (Stoner and Sandt 1991, Stoner et al. 1995). Such a competitive dynamic may buffer against a release of generalist consumer (e.g. urchins) populations that may otherwise lead to destructive overgrazing events that have been documented in a number of macrophyte communities globally (Sala et al. 1998, Rose et al. 1999, Steneck et al. 2002). A particularly interesting example of this phenomenon has been reported within kelp forest communities of California. Abalones (i.e. *Haliotis* spp.), heavily over-fished specialist grazers, have been implicated in the control of sea urchin populations (i.e. *Strongylocetrotus franciscanus, S. purpuratus*) as they are thought to reduce the relative fitness of urchins under conditions of adequate food resources (i.e. kelp detritus, "drift") through interference competition (Lowry and Pearse 1973, Tegner and Levin 1982, Karpov et al. 2001). We too show depressed urchin "fitness", as condition factor, in the presence of the specialist grazer, conch. Finally, this study intends to add to the increasing amount of literature that illustrates how the loss of community structure and trophic level heterogeneity may occur through the effects of chronic disturbances (i.e. intense overgrazing, anthropogenic nutrient enrichment) (Huxel et al. 2004, Jefferies et al. 2004, Knowlton 2004, Steneck et al. 2004).

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Literature cited

Adams, T., and R. Sterner. 2000. The effect of dietary nitrogen content on trophic level ^{15}N enrichment. Limnology and Oceanography **45**:601-607.

Beddingfield, S. D., and J. B. McClintock. 1998. Differential survivorship, reproduction, growth and nutrient allocation in the regular echinoid *Lytechinus variegatus* (Lamarck) fed natural diets. Journal of Experimental Marine Biology and Ecology **226**:195-215.

Cabana, G., and J. B. Rasmussen. 1996. Comparison of aquatic food chains using nitrogen isotopes. Proceedings of the National Academy of Science of the United States of America **93**:10844-10847.

Camp, D. K., S. P. Cobb, and J. F. van Breddveld. 1973. Overgrazing of grasses by a regular urchin, *Lytechinus variegatus*. Bioscience **23**:37-38.

Cebrian, J. D., C.M. 1998. Patterns in leaf herbivory on seagrass. Aquatic Botany **60**:67-82.

Chase, J., P. Abrams, J. Grover, S. Diehl, P. Chesson, R. Holt, S. Richards, R. Nisbet, and T. Case. 2002. Interaction between predation and competition: A review and synthesis. Ecology Letters **5**:302-315.

D'Agostino, R. B., and E. S. Pearson. 1973. Tests of departures from normality. Empirical results for the dsitribution of b_2 and $\sqrt{b_1}$. Biometrika **60**:613-622.

Dayton, P. K. 1971. Competition, disturbance, and community organization: The provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs **41**:351-391.

Deacon, J. 1973. Habitat selection and competition among abalone and sea urchin at the Sea Ranch, California. M.Sc. University fo California, Davis.

Duarte, C. M. 1995. Submerged aquatic vegetation in relation to different nutrient regimes. Ophelia **41**:87-112.

Duarte, C. M. 2000. Marine biodiversity and ecosystem services: An elusive link. Journal of Experimental Marine Biology and Ecology **250**:117-131.

Duffy, J. E. 2002. Biodiversity and ecosystem function: The consumer connection. Oikos **99**:201-219.

Duffy, J. E., K. S. MacDonald, J. M. Rhode, and J. D. Parker. 2001. Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. Ecology **82**:2417-2434.

Duffy, J. E., J. P. Richardson, and E. A. Canuel. 2003. Grazer diversity effects on ecosystem functioning in seagrass beds. Ecology Letters **6**:637-645.

Grall, J., and L. Chauvaud. 2002. Marine eutrophication and benthos: the need for new approaches and concepts. Global Change Biology **8**:813-830.

Greenway, M. 1976. The grazing of *Thalassia testudinum* in Kingston harbour, Jamaica. Aquatic Botany **2**:117-126.

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**:719-736.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist **111**:1169-1194.

Hemminga, M. A., and M. A. Mateo. 1996. Stable carbon isotopes in seagrasses: variablity in ratios and use in ecological studies. Marine Ecology Progress Series **140**:285-298.

Hughes, A. R., K. J. Bando, L. F. Rodriguez, and S. L. Williams. 2004. Relative effects of grazers and nutrients on seagrasses: a meta-analysis approach. Marine Ecology Progress Series **282**:87-99.

Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: Heterogeneity and the relative roels of bottom-up and top-down forces in natural communities. Ecology **73**:724-732.

Huxel, G., G. Polis, and R. Holt. 2004. At the frontier of the integration of food web ecology and landscape ecology. Pages 434-451 *in* G. Polis, M. Power, and G. Huxel, editors. Food webs at the landscape level. The University of Chicago Press, Chicago.

Iken, K., T. Brey, U. Wand, J. Voigt, and P. Junghans. 2001. Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. Progress in Oceanography **50**:383-405.

Jackson, D. A. 1997. Compositional data in community ecology: the paradigm or peril of proportions. Ecology **78**:929-940.

Jackson, J. B. C. 2001. What was natural in the coastal oceans? Proceedings of the National Academy of Science of the United States of America **98**:5411-5418.

Jefferies, R., R. Rockwell, and K. Abraham. 2004. Agricultural food subsidies, migratory conductivity and large-scale disturbance in arctic coastal systems: A case study. Integrative and comparative biology **44**:130-139.

Karpov, K. A., M. J. Tegner, L. Rogers-Bennett, P. E. Kalvass, and I. K. Taniguchi. 2001. Interactions among red abalones and sea urchins in fished and reserve sites of northern California: Implications of competition to management. Journal of shellfish research **20**:743-753.

Keller, B. D. 1983. Coexistence of sea urchins in seagrass meadows: An experimental analysis of competition and predation. Ecology **64**:1581-1598.

Keselman, H. J. 1976. A power comparison of the Tukey multiple comparison statistic. Edu. Psychol. Meas. **36**:97-104.

Knowlton, N. 2004. Multiple "stable" states and the conservation of marine ecosystems. Progress in Oceanography **60**:387-396.

Lawrence, J. 1975. On the relationship between marine plants and sea urchins. Oceanography and Marine Biology: an Annual Review **13**:213-286.

Lowry, L. F., and J. S. Pearse. 1973. Abalones and sea urchins in an area inhabited by sea otters. Marine Biology **23**:213-219.

MacArthur, R., and E. O. Wilson. 1967. The Theory of Island Biogeography. Rrinceton University Press, Princeton, New Jersey.

Macia, S., and D. Lirman. 1999. Destruction of Florida Bay seagrasses by a grazing front of sea urchins. Bulletin of Marine Science **65**:593-601.

McCann, K., A. Hastings, and D. Strong. 1998. Trophic cascades and trophic trikles in pelagic food webs. Proc. R. Soc. Lond. B. **265**:205-209.

McClelland, J. W., I. Valiela, and R. H. Michener. 1997. Nitrogen-stable isotope signatures in esturine food webs: A record of increasing urbanization in coastal watersheds. Limnology and Oceanography **42**:930-937.

McGlathery, K. J. 1995. Nutrient and grazing influences on a subtropical seagrass community. Marine Ecology Progress Series **122**:239-252.

Moore, J., E. Berlow, D. Coleman, P. de Ruiter, Q. Dong, A. Hastings, N. Collins-Johnson, K. McCann, K. Melville, P. Morin, K. Nadelhoffer, A. Rosmond, D. Post, J. Sabo, K. Scow, M. Vanni, and D. Wall. 2004. Detritus, Trophic Dynamics, and Biodiversity. Ecology Letters **7**:584-600.

Ogden, J. C. 1980. Faunal relationships in Caribbean seagrass beds. Pages 173-198 *in* R. Phillips and C. McRoy, editors. Handbook of seagrass biology: An ecosystem perspective. Garland STPM Press, New York.

Paine, R. T. 1980. Food webs: Linkage, interaction strength and community infrastructure. Journal of Animal Ecology **49**:667-685.

Patriquin, D. G. 1975. "Migration" of blowouts in seagrass beds at Barbados and Carriacou, West Indies, and its ecological and geological implications. Aquatic Botany **1**:163-189.

Persson, L. 1999. Trophic Cascades: abiding heterogeneity and the trophic level concept at the end of the road. Oikos **85**:385-397.

Polis, G. A., M. E. Power, and G. R. Huxel. 2004. Food webs at the landscape level. The University of Chicago Press, Chicago.

Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. American Naturalist **147**:813-846.

Randall, J. E. 1965. Grazing effect on seagrasses by herbivorous reef fishes in the West Indies. Ecology **46**:255-260.

Regis, M. 1986. Microstructure adaptive des radioles de Paracentrotus lividus (Echinodermata: Echinoidea) en milieu eutrophise par des eaux usees. Marine Biology **90**:271-277.

Rose, C. D., W. C. Sharp, W. J. Kenworthy, J. H. Hunt, W. Lyons, G,, E. J. Prager, J. F. Valentine, M. O. Hall, P. E. Whitfield, and J. W. Fourqurean. 1999. Overgrazing of a large seagrass bed by the sea urchin *Lytechinus variegatus* in Outer Florida Bay. Marine Ecology Progress Series **190**:211-222.

Sala, E., C. F. Boudouresque, and M. Harmelin-Vivien. 1998. Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. Oikos **82**:425-439.

Short, F. T., and S. Wyllie-Echeverria. 1996. Natural and human-induced disturbance of seagrasses. Environmental Conservation **23**:17-27.

Siddon, C. E., and J. D. Witman. 2003. Influence of chronic, low-level hydrodynamic forces on subtidal community structure. Marine Ecology Progress Series **261**:99-110.

Sousa, W. P. 2000. Natural disturbance and the dynamics of marine benthic communities. Pages 85-130 *in* M. D. Bertresss, S. D. Gaines, and M. E. Hay, editors. Marine Community Ecology. Sinauser Associates.

Steneck, R. S., and M. N. Dethier. 1994. A functional group approach to the structure of algal-dominated communities. Oikos **69**:476-498.

Steneck, R. S., M. Graham, B. Bourque, D. Corbett, J. Erlandson, J. Estes, and M. Tegner. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. Environmental Conservation **29**:436-459.

Steneck, R. S., J. Vavrinec, and A. V. Leland. 2004. Accelerating trophic-level dysfunction in kelp forest ecosystems of the Western North Atlantic. Ecosystems **7**:323-332.

Stoner, A. W., M. Ray, and J. M. Waite. 1995. Effects of a large herbivorous gastropod on macrofauna communities in tropcal seagrass meadows. Marine Ecology Progress Series **121**:125-137.

Stoner, A. W., and V. J. Sandt. 1991. Experimental analysis of habitat quality for juvenile queen conch in seagrass meadows. Fishery Bulletin **89**:693-700.

Stoner, A. W., and J. M. Waite. 1991. Trophic biology of *Strombus gigas* in nursery habitats: Diets and food sources in seagrass meadows. J Moll. Stud. **57**:451-460.

Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology **73**:747-754.

Tegner, M. J., and L. A. Levin. 1982. Do sea urchins and abalones compete in California? Pages 265-271 *in* J. M. Lawrence, editor. International Echinoderms Conference. A.A. Balkema, Rotterdam, Netherlands, Tampa Bayida, Florida.

Tribble, G. W. 1981. Reef-based herbivores and the distribution of two seagrasses (*Syringodium filiforme* and *Thalassia testudinum*) in the San Blas Islands (Western Caribbean). Marine Biology **65**:277-281.

Vadas, R. L., T. Fenchel, and J. C. Ogden. 1982. Ecological studies of the sea urchin, Lytechinus variegatus, and the algal-seagrass communities of the Miskito Cays, Nicaragua. Aquatic Botany **14**:109-125.

Vaitilingon, D., R. Rasolofonirina, and M. Jangoux. 2003. Feeding preferences, seasonal gut repletion indices, and diel feeding patterns of the sea urchin Trpnuestes gratilla (Echinodermata:Echinoidea) on a coastal habitat off Toliara (Madagascar). Marine Biology **143**:451-458.

Valentine, J. F., and K. L. Heck. 1991. The role of sea urchin herbivory 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.

Valentine, J. F., and K. L. Heck. 1999. Seagrass herbivory: Evidence for continued grazing of marine grasses. Marine Ecology Progress Series **176**:291-302.

Valentine, J. F., and K. L. Heck. 2001. The role of leaf nitrogen content in determining turtlegrass (Thalassia testudinum) grazing by a generalized herbivore in the northeastern Gulf of Mexico. Journal of Experimental Marine Biology and Ecology **258**:65-86.

Valentine, J. F., K. L. Heck, K. D. Kirsch, and D. Webb. 2000. Role of sea urchin *Lytechinus variegatus* grazing in regulating subtropical turtlegrass *Thalassia testudinum* meadows in the Florida Keys (USA). Marine Ecology Progress Series **200**:213-228.

Vetter, E., and P. Dayton. 1999. Organic enrichment by macrophyte detritus and abundance patterns of megafaunal populations in submarine canyons. Marine Ecology Progress Series **186**:137-148.

Vizzini, S., G. Sara, R. H. Michener, and A. Mazzola. 2002. The role and contribution of seagrass *Posidonia oceanica* (L.) Delile organic matter for secondary consumers as revealed by carbon and nitrogen stable isotope analysis. Acta Oecologica **23**:277-285.

Williams, S. L. 1987. Competition between the seagrasses *Thalassia testudinum* and *Syringodium filiforme* in a Caribbean lagoon. Marine Ecology Progress Series **35**:91-98.

Williams, S. L. 1990. Experimental studies of Caribbean seagrass bed development. Ecological Monographs **60**:449-469.

Zar, J. H. 1999. Biostatistical Analysis, 4th edition. Prentice -Hall, Inc., London.

Tables

Table 1a: Results of two-way and one-way ANOVAs for percent resources (arcsine -square root transformed) present in experiment one (4 x 5 factor, see Fig 2a) conducted in the South-western Dominican Republic. Bold p-values are less than 0.05.

Factor	df	SS	MS	F	P
Detritus					
Habitat x Herbivory	12	894	74.5	0.435	0.939
Error	40	6858	171.5		
Herbivory	4	3577	894.3	20.708	**< 0.001**
	Tukey HSD Multiple Comparisons				
	1 vs 3				**0.015**
	1 vs 5				**< 0.001**
	2 vs 5				**< 0.001**
	3 vs 5				**< 0.001**
	4 vs 5				**< 0.001**
Habitat	3	1936	645.5	14.946	**< 0.001**
	Tukey HSD Multiple Comparisons				
	A vs B				**< 0.001**
	A vs D				**0.029**
	B vs C				**<0.001**
Error	45	1943	43.2		
Thalassia					
Habitat x Herbivory	12	1503.618	125.302	0.557	0.863
Error	40	8995.705	224.893		
Herbivory	4	4561.127	1140.282	19.494	**< 0.001**
	Tukey HSD Multiple Comparisons				
	1 vs 5				**< 0.001**
	2 vs 5				**< 0.001**
	3 vs 5				**< 0.001**
	4 vs 5				**< 0.001**
Habitat	3	2549.953	849.984	14.531	**< 0.001**
	A vs C				**< 0.001**
	A vs D				**< 0.001**
	B vs C				**0.003**
Error	45	2632.209	58.494		
Syringodium					
Habitat x Herbivory	12	1675.137	139.595	1.401	0.206
Error	40	3984.759	99.619		
Herbivory	4	1115.941	278.985	5.494	**0.001**
	Tukey HSD Multiple Comparisons				
	2 vs 4				**0.041**
	2 vs 5				**0.001**
	3 vs 5				**0.031**
Habitat	3	1578.807	526.269	10.363	**<0.001**
	Tukey HSD Multiple Comparisons				
	A vs D				**<0.001**
	B vs D				**<0.001**
	C vs D				**0.001**
Error	45	2285.231	50.783		

Table 1b: Results of two-way and one-way ANOVAs for percent resource (arcsine - square root transformed) in experiment two (2 x 4 factor) conducted in the South-western Dominican Republic. Bold p-values are less than 0.05.

Factor	df	SS	MS	F	P
Detritus					
Habitat x Herbivory	3	1088.9	262.9	1.721	0.197
Error	19	4006.9	210.9		
Herbivory	3	1703.1	567.7	6.405	**0.004**
	Tukey HSD Multiple Comparisons				
	0 vs 5				0.06
	1 vs 5				**0.002**
	3 vs 5				0.066
Habitat	1	1538.292	1538.292	17.36	**0.001**
	Tukey HSD Multiple Comparisons				
	A vs D				**0.001**
Error	18	1595.4	88.6		
Thalassia					
Habitat x Herbivory	3	1061.4	353.8	1.211	0.333
Error	19	5549.4	292.1		
Herbivory	3	1760	586.8	7.637	**0.002**
	Tukey HSD Multiple Comparisons				
	0 vs 5				**0.041**
	1 vs 5				**0.001**
	3 vs 5				**0.011**
Habitat	1	3077.952	3077.952	40.06	**< 0.001**
	A vs D				**< 0.001**
Error	18	1383.1	76.84		
Syringodium					
Habitat x Herbivory	3	297.9	99.3	0.885	0.487
Error	19	2132.5	112.2		
Herbivory	3	218.2	72.7	3.291	**0.044**
	Tukey HSD Multiple Comparisons				
	3 vs 5				**0.034**
Habitat	1	1734.652	1734.652	78.5	**< 0.001**
	Tukey HSD Multiple Comparisons				
	A vs D				**< 0.001**
Error	18	397.9	22.1		

Table 2: Results of two-way ANOVA for condition factor in experiment one conducted at site 1 (2a) and site 2 (2b) in the South-western Dominican Republic. Bold p-values are less than 0.05. Bold pair-wise comparisons (e.g. A3 vs D3) for urchin condition in experiment one (2a) indicate those discussed in the text

2a)

Factor	df	SS	MS	F	P
conch condition					
Habitat	2	0.017	0.009	5.26	**0.009**
Herbivory	1	0.005	0.005	2.79	0.101
Habitat x Herbivory	2	0.005	0.002	1.43	0.249
Error	47	0.079	0.002		
	Tukey HSD Multiple Comparisons				
	A vs B				0.068
	A vs C				**0.009**
	B vs C				**0.63**
urchin condition					
Habitat x Herbivory	10	0.105	0.010	20.36	**< 0.001**
Error	169	0.087	0.000		
	Tukey HSD Multiple Comparisons				
	A3 vs C5				**0.029**
	A3 vs D3				**< 0.001**
	A3 vs D5				**< 0.001**
	A4 vs D5				**< 0.001**
	A5 vs B3				**0.0158**
	A5 vs C3				**< 0.001**
	A5 vs D5				**< 0.001**
	B3 vs C5				**0.0026**
	B3 vs D3				**< 0.001**
	B3 vs D5				**< 0.001**
	B4 vs D5				**0.006**
	B5 vs C3				**< 0.001**
	B5 vs D5				**< 0.001**
	C3 vs C4				**0.034**
	C3 vs C5				**< 0.001**
	C3 vs D3				**< 0.001**
	C3 vs D5				**< 0.001**
	C4 vs D5				**0.013**
	C5 vs D5				**< 0.001**

2b)

Factor	df	SS	MS	F	P
conch condition					
Habitat x Herbivory	1	0.144	0.144	10.4	**0.003**
Error	32	0.445	0.014		
	Tukey HSD Multiple Comparisons				
	A0 vs D0				**0.003**
urchin condition					
Habitat	1	0.039	0.039	40.77	**< 0.001**
Herbivory	2	0.026	0.013	13.61	**< 0.001**
Habitat x Herbivory	2	0.001	0.000	0.687	0.505
Error	165	0.159	0.0009		
	Tukey HSD Multiple Comparisons				
	A vs D				**< 0.001**
	3 vs 5				**0.018**
	5 vs 0				**< 0.001**

Table 3: Results of two-way and one-way ANOVA for interaction strength in experiment one conducted at site 1 in the South-western Dominican Republic. Bold p-values are less than 0.05. Bold pair-wise comparisons (e.g. A3 vs D3) for interactions strengths with *Syringodium* (e.g. C2 vs C3) indicate those discussed in the text in detail.

Factor	df	SS	MS	F	P
Detritus					
Habitat x Herbivory	9	0.208	0.023	1.727	0.09
Error	116	1.554	0.013		
Habitat	3	0.165	0.055	4.497	**0.005**
	Tukey HSD Multiple Comparisons				
	A vs. D				**0.0037**
Herbivory	3	0.118	0.039	3.201	**0.025**
	Tukey HSD Multiple Comparisons				
	3 vs 5				**0.0241**
Error	119	1.458	0.0122		
Thalassia					
Habitat x Herbivory	9	0.0787	0.0087	1.475	0.165
Error	116	0.687	0.0059		
Habitat	3	0.0366	0.0122	2.117	0.102
Herbivory	3	0.0221	0.0073	1.278	0.285
Error	119	0.6865	0.0057		
Syringodium					
Habitat x Herbivory	9	1.881	0.2089	8.0314	**<0.0001**
Error	116	3.017	0.026		
	Tukey HSD Multiple Comparisons				
	A2 v C2				**0.032**
	A2 v C3				**<0.001**
	B2 v C2				**<0.001**
	C2 v A3				**0.031**
	C2 v C3				**<0.001**
	C2 v D3				**<0.001**
	C2 v A4				**<0.001**
	C2 v B4				**<0.001**
	C2 v C4				**<0.001**
	C2 v A5				**<0.001**
	C2 v B5				**<0.001**
	C2 v C5				**<0.001**
	C2 v D5				**<0.001**
	A3 v C3				**<0.001**
	A3 v A4				**<0.001**
	B3 v C3				**0.002**
	C3 v A5				**0.01**
	C3 v B5				**0.004**
	C3 v D5				**0.006**
	A4 v D5				**0.036**

Figures

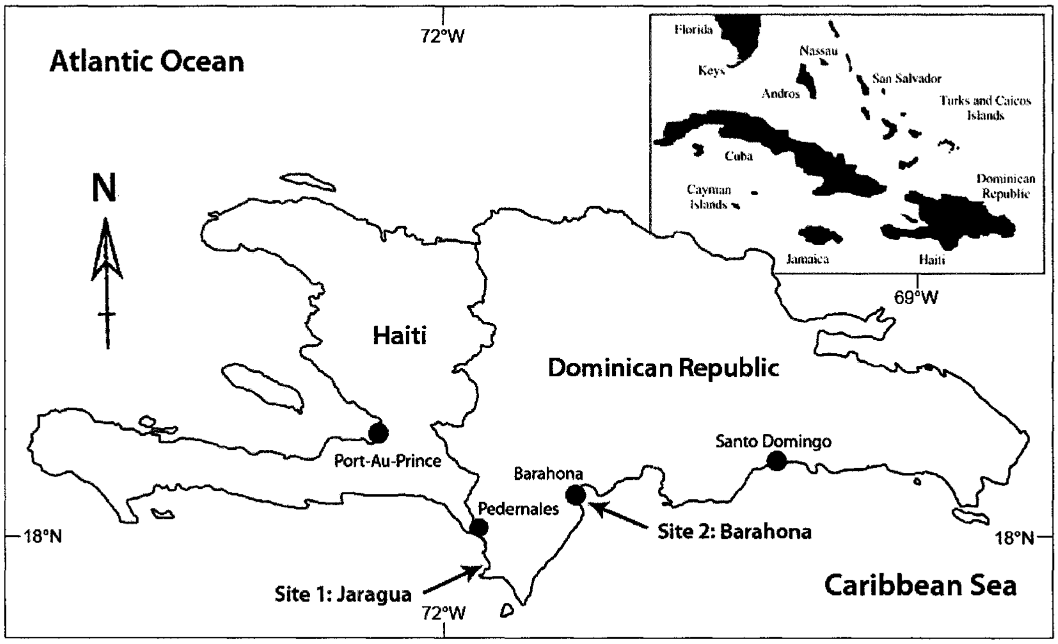


Fig. 1: Map of Hispaniola (Inset: location of Hispaniola in the Central Caribbean). Experimental treatments conducted at two sites in South-western Dominican Republic. Site 1 – Jaragua National Park (See Figure 2a for treatments conducted), Site 2 – Embayment in front of Barahona, provincial capital (See Figure 2b for treatments conducted).

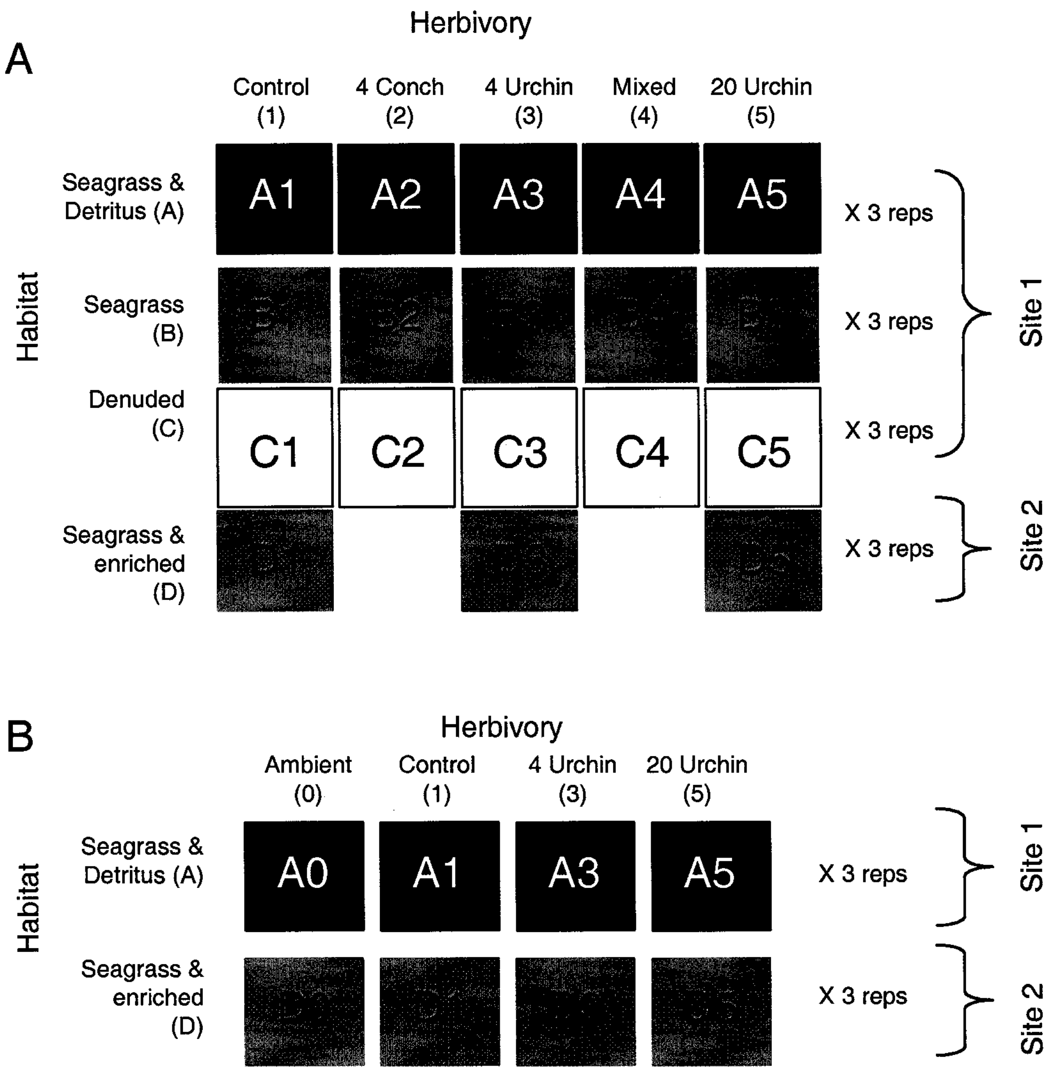


Fig. 2: Enclosure treatments conducted at Parque Nacional Jaragua (site 1) and Barahona (site 2), South-western, Dominican Republic. Letter and number codes denote habitat/resources and herbivory treatments respectively. All enclosures were one metre square. Control (1) denotes all mega-invertebrate consumers removed, values beside consumers indicate density, Mixed denotes 2 conch and 2 urchins, all D treatments conducted at site 2. A) Two factor experiments (3 x 5) of habitat/resources and herbivory all conducted at site 1. B) Two factor experiment (2 x 4) of habitat/resources and herbivory with addition of ambient treatments (0). Ambient treatments were not enclosed but data collected in the immediate area of experiments.

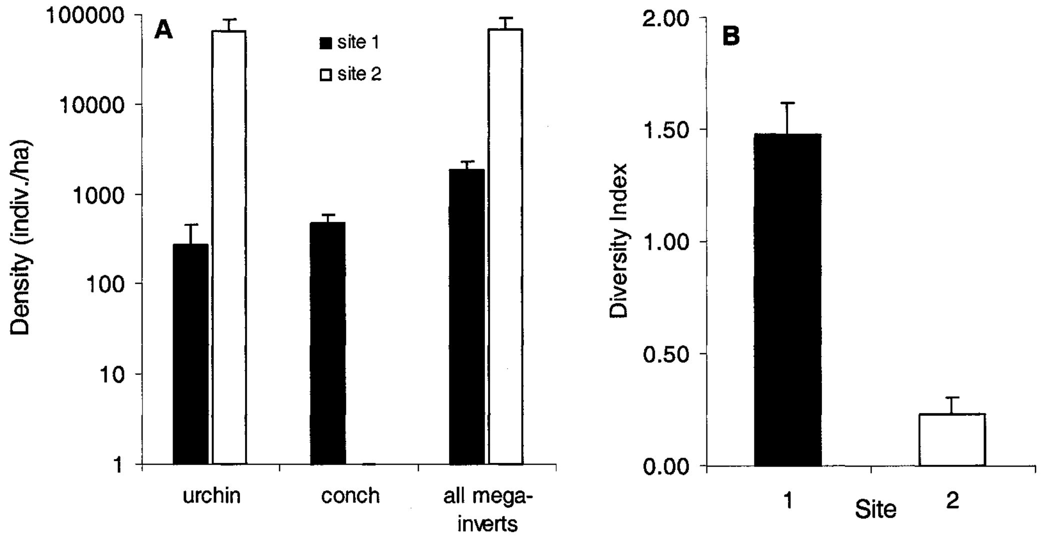


Fig. 3: Mean (± 1 se) values for mega-invertebrates statistics at site 1 (low nutrient enrichment) and site 2 (high nutrient enrichment), Southwestern, Dominican Republic. A) Density (indiv./ha) of conch (*Strombus gigas*), urchins (*Lytechinus variegatus*) and total mega-invertebrate consumer community (14 species or species groups: urchins; heart urchins, sand dollars; sea stars, gastropods, sea cucumbers, bivalves etc.) observed. B) Diversity index of mega-invertebrate consumers calculated using the Shannon-Weiner index. All paired t-test results (site 1 vs. site 2) for consumer density (log n+10) and diversity (untransformed) were significant ($P < 0.005$).

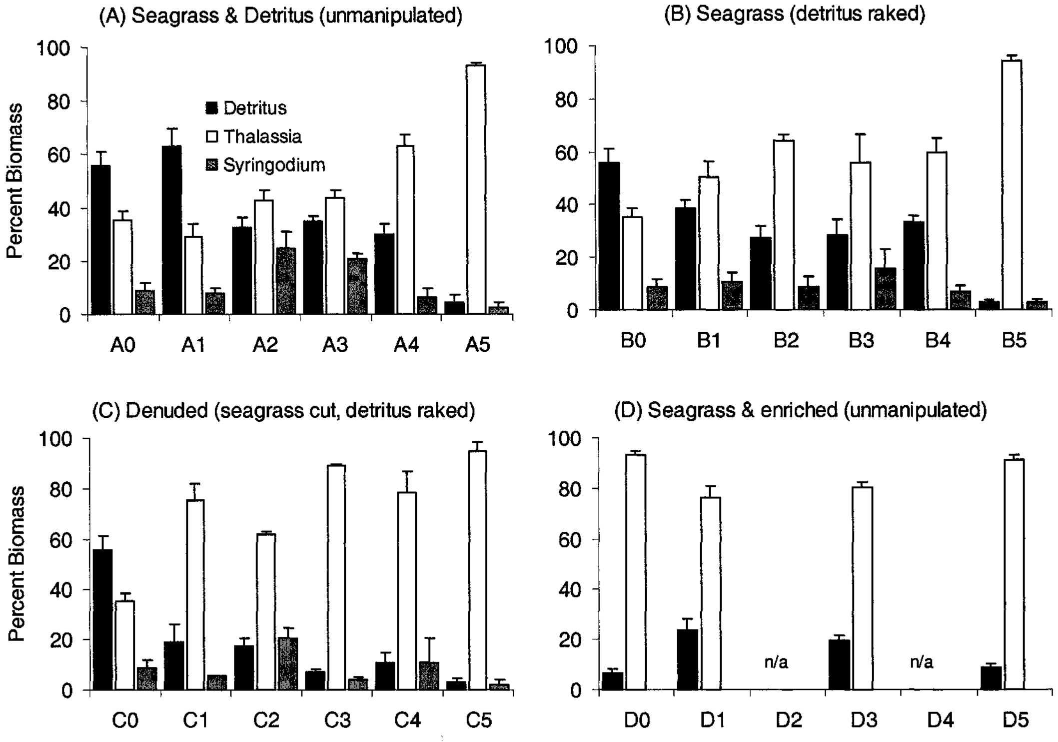


Fig. 4: Mean (± 1 se), n=3, percent biomass of macrophyte resources in all treatments at the end of experiments in South-western Dom. Rep. (14 weeks, except 20 urchin treatments, 10 weeks). Percents based on gDW/m^2 of particular resource to total biomass. Treatments represent various combinations of habitat/resources (A, B, C, D) and herbivory (open, control, conch, low urchins, mixed, and high urchin density) See Fig. 2 for details. See table 1 for details of ANOVA and pairwise comparisons.

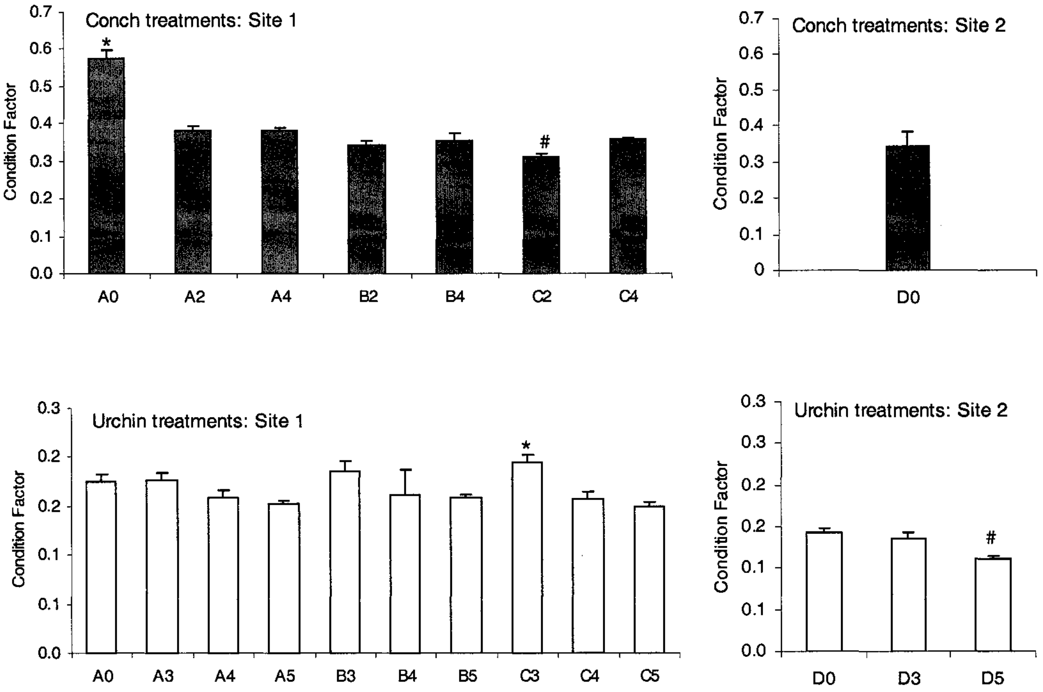


Fig 5: Mean condition factor (± 1 se), n=3, of *Strombus gigas* (filled bars) and *Lytechinus variegatus* (open bars) over various experimental treatments at site 1 (low nutrients) and site 2 (high nutrients) in the South-western, Dominican Republic. Habitat/resource treatments: A = unmanipulated; B = detritus raked; C = denuded; D (site 2) = unmanipulated, low detritus, high nutrients. Herbivore treatments: 0 = ambient; 2 = 4 conch; 3 = 4 urchins; 4 = 2 conch & 2 urchins; 5 = 20 urchins. Details of multi-factorial analysis and pairwise comparisons may be seen in Table 2. * and # indicate highest and lowest condition factor respectively for *Strombus gigas* and *Lytechinus variegates.*

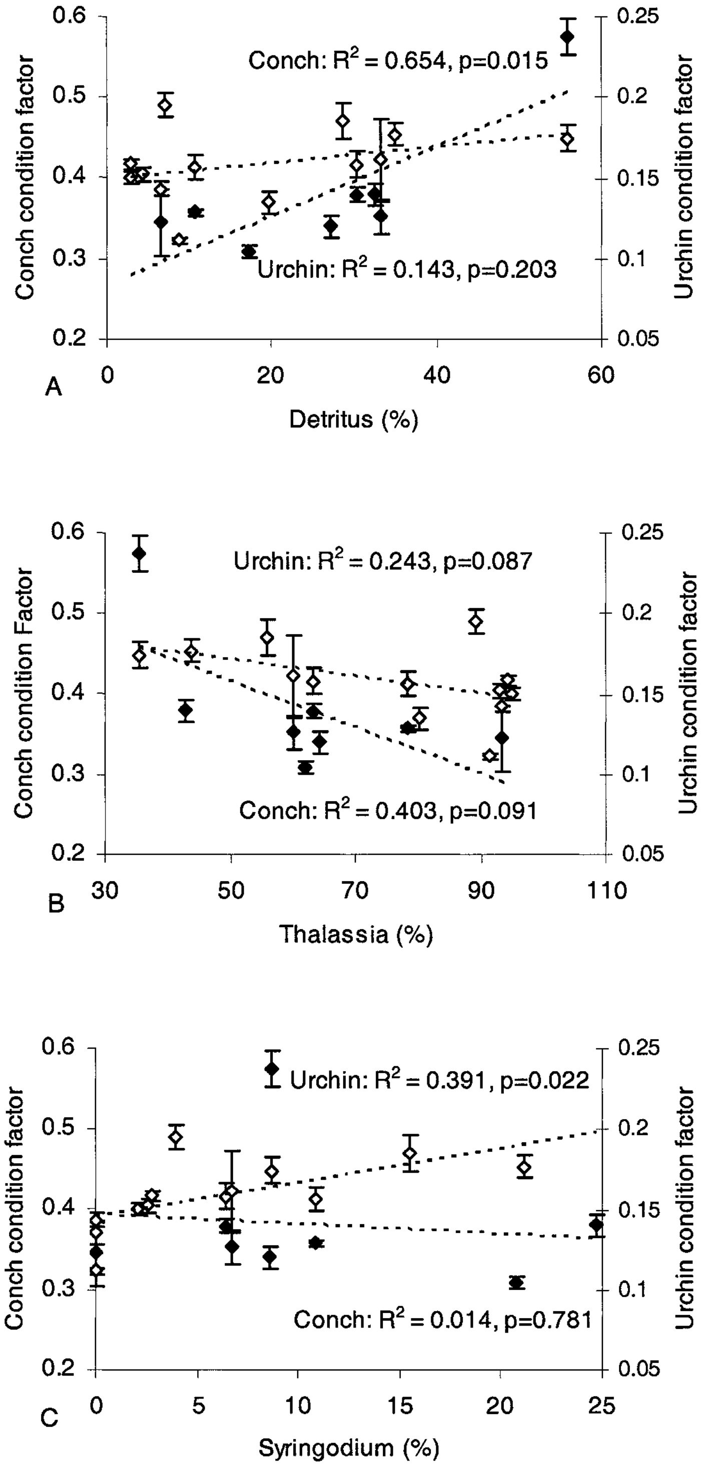
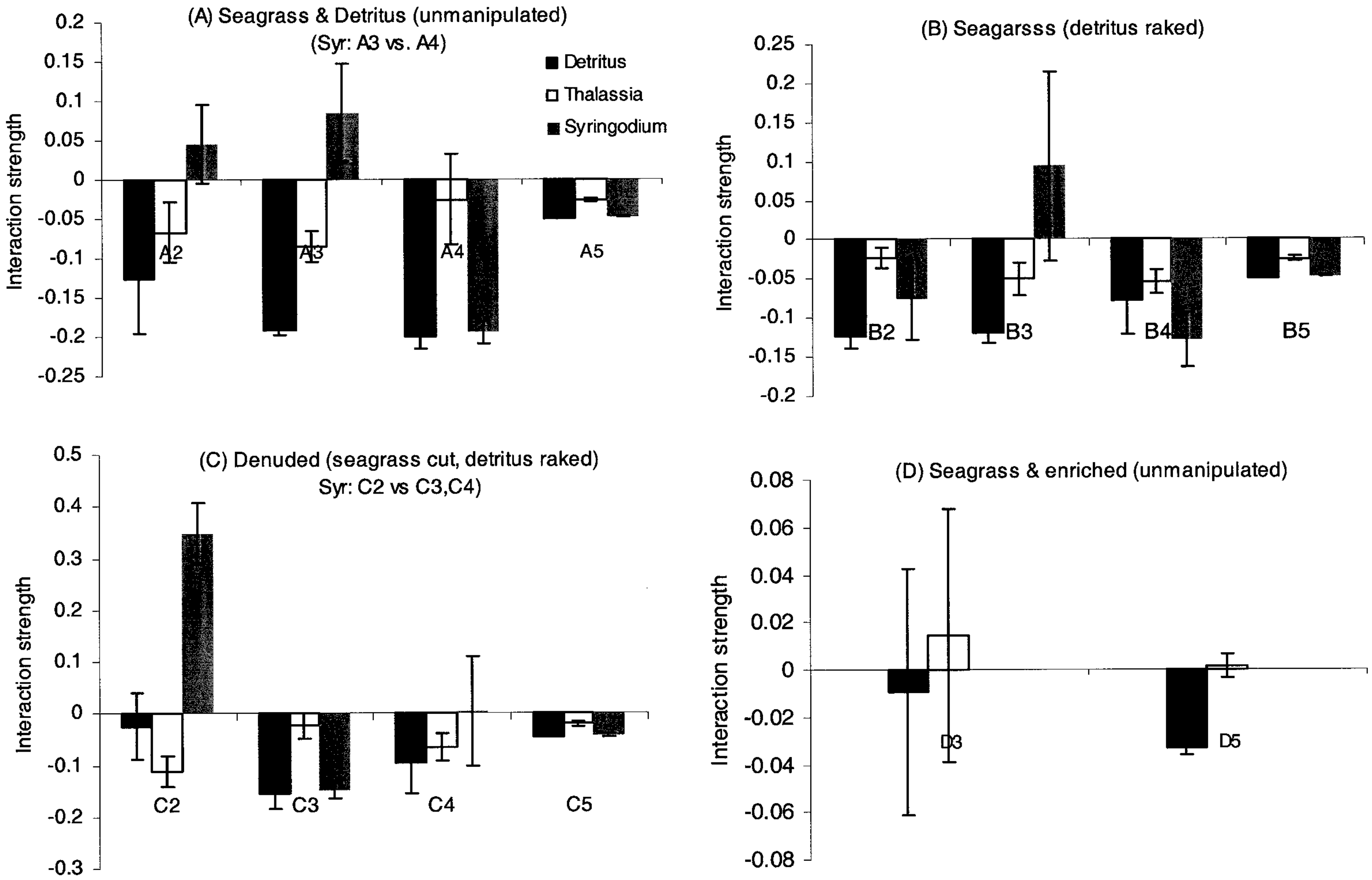


Fig. 6: Mean percent resource (± 1 se), n=3, present versus condition factor of *Strombus gigas* (filled symbols) and *Lytechinus variegatus* (open symbols) with associated regression analysis. A) Detritus, B) *Thalassia*, C) *Syringodium*.



(A) Seagrass & Detritus (unmanipulated)
(Syr: A3 vs. A4)

(B) Seagarsss (detritus raked)

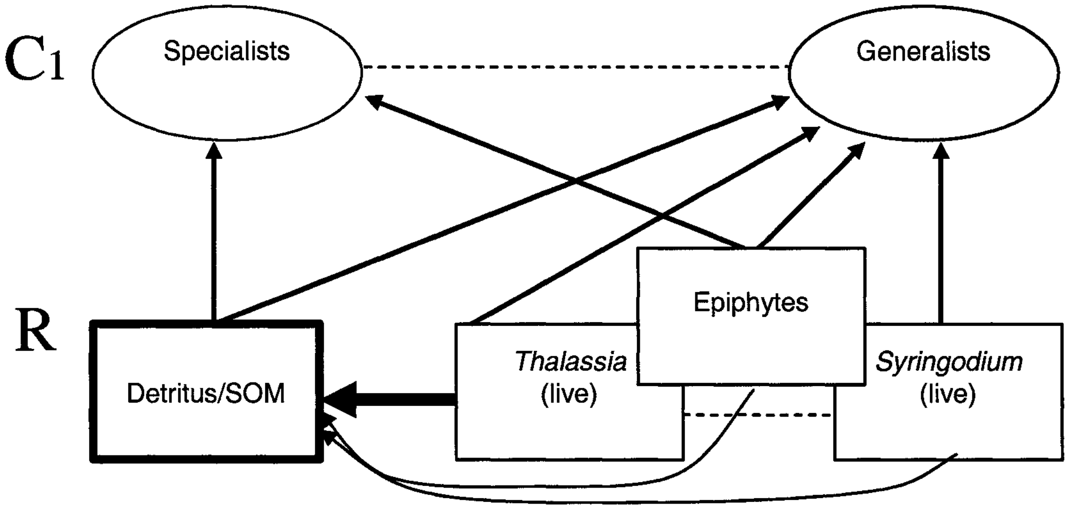
(C) Denuded (seagrass cut, detritus raked)
Syr: C2 vs C3,C4)

(D) Seagrass & enriched (unmanipulated)

Fig. 7: Mean interaction strength (per capita, predator) (± 1 se) (n=9) grouped by habitat/resource treatments (A, B, C, D). Herbivore treatments (2 = 4 conch, 3 = 4 urchins, 4 = 2 conch & 2 urchins, 5 = 20 urchins). Details of ANOVA and pairwise comparisons may be seen in Table 3.

Appendices

Appendix 1: Simplified schematic of sub-web examined using enclosure experiments. Polygons are resources (R): *Thalassia* and *Syringodium* seagrass; detritus and sediment organic material (SOM); epiphytes resident on seagrass leaves. Ovals are consumers (C): Specialists - Queen conch (*Strombus gigas*); Generalists - sea urchin (*Lytechinus variegatus*). Arrows represent energy flow. Dotted line within trophic level represents competition (exploitative, interference) and/or intra-guild predation.



Connecting Statement

In the preceding chapter, I examined the effect of a number of chronic disturbance regimes on an important sub-web of ubiquitous species of producers and consumers, and associated life history strategies, in Caribbean seagrass beds. This study revealed the dominance of stress-tolerant generalists, most notably extremely elevated levels of urchins, which seem to overgraze traditional resources (e.g. autochthonous seagrass detritus) and benefit either directly or indirectly from chronic nutrient enrichment (i.e eutrophication) through the introduction of allochthonous resources which increase production via nutrient enrichment. In addition, I present evidence of interference competition between specialist conch and generalist urchins, under pristine conditions (i.e. high detritus, preferred resource), that results in urchins switching to secondary resources. This dynamic illustrates the importance of trophic heterogeneity in general which specifically results in "buffering" the over-consumption of diversity enhancing seagrass detritus and living seagrass by urchins that has been documented in other macrophyte systems.

In the following chapter, I investigate the pattern of producer and consumer functional group "succession" that occurs across a wide gradient of increasing nutrient enrichment using eleven seagrass beds located throughout the Caribbean. The increasing nutrient enrichment is again associated with significant declines in both autochthonous detritus and overall mega-invertebrate consumer diversity (i.e. trophic heterogeneity), including the loss of the specialist grazers (i.e. *Strombus* spp.) as well as tremendous increases in generalist consumers at the highest nutrient inputs. The allochthonous sources of nutrients to seagrass beds from increased urbanization in adjacent watersheds may allow such drastic or "catastrophic" state shifts to remain stable even as elevated levels of generalist consumers suppress autochthonous resources.

Abstract

Allochthonous, anthropogenic nutrient enrichment, in aquatic ecosystems globally, has resulted in significant and sometimes catastrophic changes in food web structure. Although such changes have been associated with the loss of diversity and ecosystems services, and may in fact lead to alternate states, little empirical work has been done to study food webs of similar systems across a continuous gradient of nutrient enrichment. In this study, eleven seagrass beds in Barbados, Dominican Republic and Panama were positioned along a gradient of relatively increasing nutrient enrichment using the relationship between human population density and the stable isotope, ^{15}N, in tissues of common, long-lived benthic primary consumers. Detailed quantitative sampling of biomass and density, for resources and consumers respectively, were conducted in an effort to understand how food webs change. The resulting patterns of increasing consumer density and decreasing consumer diversity corresponded well to the loss of autochthonous pools of detritus. At very high levels of enrichment (i.e. eutrophication) the community was dominated (> 90%) by stress tolerant/competitive producers (*Thalassia testudinum*) and very high densities of generalist echinoid consumers (> 66000/ha, >98%). This is likely made possible by the emergence of alternative resources in the form of donor-controlled, allochthonous phytoplankton detritus or possible expansions in the production of autochthonous seagrass epiphytes and stress-tolerant/ competitive seagrass (i.e. *Thalassia testudinum*). The availability of such new and expanded resources, and the suspected use of them by generalist consumers, is a result of high levels of run-off (e.g. organic pollution) from the adjacent watershed where human populations exceed 1000 persons per km^2. The recognition and inclusion of donor-controlled resources into food webs is critical if we are to untangle such structures and begin to understand how we may alleviate problems resulting from anthropogenic disturbances.

Introduction

During the 1970's ecologists began the task of mapping out the elaborate structure of real food webs (Cohen *et al.* 1990). A number of food webs have been quite thoroughly documented and researchers have spent much effort in comparing these food webs in search of ubiquitous structure (Martinez 1991). Due perhaps to the limited nature of food web data, little effort has been spent on comparing food webs of a similar system (e.g. seagrass) across an environmental gradient. However, such empirical analysis could significantly aid in our understanding of how ecosystems and food webs change with respect to modern anthropogenic influences.

A number of researchers have highlighted how widespread anthropogenic disturbances, in particular nutrient loading, often lead to drastic changes in ecosystems (Hughes 1994; Jackson 2001; Scheffer *et al.* 2001). More importantly, they have found evidence that once the ecosystem is altered it may become very difficult to return the system back to its original state by simply reducing perturbations (Scheffer *et al.* 2001). The "catastrophe" ecosystem theory that emerges from this research suggests that major functional groups in the food web also change dramatically, and in doing so drive ecosystem level changes that feedback to maintain the system in this new altered state. As an example, lake researchers have found that eutrophication of small lakes frequently flips the lake from a clear state to a turbid state (Scheffer *et al.* 1993; Carpenter *et al.* 1999). Among other physical changes, this turbid lake state prevents light penetration and so diminishes the ability for the benthic macrophytes of the clear lake state to return. Restoration efforts become non-trivial and costly - simply reducing nutrient loading is frequently not enough. Such examples suggest that we must begin to understand how food web structure and function are altered across environmental gradients, especially gradients that reflect human impacts through time (e.g., nutrient loading, fragmentation, etc.).

Here, we empirically explore the implications of increased nutrient enrichment on Caribbean seagrass food webs. These coastal marine ecosystems may be especially prone to the effects of human development since urbanization, and associated organic run-off, tends to be most dramatic on coasts (McClelland *et al.* 1997; Cloern 2001). As with lakes, increased nutrient inputs (i.e. eutrophication) may play a major role in re-structuring the food web. Recent theory on the role of such inputs (i.e. allochthonous forms) suggests that generalist consumers frequently tap into these alternative energy supplies fuelling significant changes in the dominance of species in these food webs (Polis & Strong 1996). Furthermore, the donor-control aspect (i.e. consumers do not affect resource renewal rate) of these interactions with generalist consumers may frequently be stable (Huxel & McCann 1998). This despite the fact that increased generalist consumer density drives heightened suppression (e.g. overgrazing) of autochthonous resources which receive the majority of the input (e.g. nutrients). A classic example of this phenomenon is seen by the tremendous influence of snow geese on the Hudson Bay lowland ecosystem (Jefferies 2000). Here, increases in southern agriculture and associated use of fertilizers has subsidized snow goose populations and led to the top-down suppression of the Hudson Bay flora as well as associated declines in soil invertebrate assemblages and some shore bird populations (Jefferies 2000). The ecosystem, denuded beyond recognition, appears to have simultaneously altered the detrital pathway and other important ecosystem level properties (e.g., salinity, erosion etc.).

Food web ecologists have largely ignored the role detrital pathways play in the diversity and structuring of food webs (Polis & Strong 1996; Moore *et al.* 2004). Detritus and associated pathways form rich alternative energy sources, drive nutrient recycling and provide complex habitat structure that should influence diversity, community structure and dynamics (Moore *et al.* 2004). Food web ecology lacks a well-developed theory for the role of detritus (although see (DeAngelis 1992) while few empirical studies have been carried out to elucidate the patterns in detrital food web structure of ecosystems.

Caribbean Seagrass Food Webs

Extensive exploitation of marine species has occurred within the Caribbean seagrass-coral reef-mangrove habitat complex over the last three centuries resulting in major changes in food web structure (Jackson *et al.* 2001). During the last 50 years extensive overfishing has continued with removals of large and intermediate predators as well as many herbivorous species (Hughes 1994; Jackson *et al.* 2001). Most recently, increases in human populations and associated urbanization along coastlines have caused significant nutrient loading in these systems (Duarte 1995; Short & Wyllie-Echeverria 1996; Jackson 2001). Nutrient loading combined with continued over-harvesting may work synergistically towards habitat degradation and trophic cascades leading to simplified food webs, homogenized landscapes, and loss of ecosystem services (Hughes 1994; Carpenter *et al.* 1999; Jackson 2001).

It is important to note that during this period of continued overexploitation and increased nutrient loading generalist herbivorous urchins, notably *Lytechinus variegatus*, have been observed extensively grazing living seagrass (Camp *et al.* 1973; Valentine & Heck 1991; Rose *et al.* 1999). Although destructive overgrazing seems rare at this time, the negative impact of such activity has been documented with the almost complete loss of the seagrass detritus and the living structural framework both above and below ground (Camp *et al.* 1973; Rose *et al.* 1999; Peterson *et al.* 2002). Such widespread changes would likely make seagrass meadows quite unsuitable to most species. The loss of traditional seagrass systems would also affect a number of ecosystem services including their use as nursery and foraging habitats, nutrient recycling, sediment stabilization and exports of significant production to mangroves and coral reef food webs (Jackson 2001).

In this study, consistent with our interest in considering food webs as a function of changing conditions, we will examine the response of seagrass food webs to enrichment along a gradient of human population density. We first examine the level of nutrient enrichment in seagrass food webs as a function of human population densities within watersheds. The data suggests that nutrient levels are increased where human densities are high. We then empirically consider how altered nutrient levels correlate to attributes of seagrass community structure including abundance of benthic resources, with special attention to autochthonous detritus, and mega-invertebrate consumer functional groups. Seagrass communities should become greatly simplified or homogenized with increased nutrients, such that these impacted ecosystems have little, if any, detritus, low plant and animal diversity, and substantially increased densities of generalist consumers (i.e., sea urchins) which are tolerant to pollution stress and flexible to changes in habitat and associated food resource availability. The significant changes in seagrass ecosystems (e.g., lack of detritus) may present another case for catastrophic ecosystem change although much further work is needed.

Materials & Methods

Human Populations & Nutrient Enrichment

The naturally occurring heavy isotope of nitrogen (^{15}N) allows the trophic position of organisms from a wide variety of taxa to be determined with reasonable confidence (Peterson & Fry 1987; Hobson & Welch 1992). Stable isotope ratios ($^{15}N/^{14}N$) are expressed in delta units (δ) and defined as parts per thousand ($^{o}/_{oo}$) deviations from atmospheric nitrogen. Consumers acquire stable isotope signatures through their diet with nitrogen ($\delta^{15}N$) pools of animals enriched by approximately 3.4 $^{o}/_{oo}$ relative to their diet (Peterson & Fry 1987).

In the past, comparisons of trophic structure across systems were complicated by variation in $\delta^{15}N$ at the base of foodwebs. This variation has been resolved by illustrating that $\delta^{15}N$ increases significantly with human population densities in watersheds (Cabana & Rasmussen 1996). The high trophic position of humans, expressed through sewage-derived nutrients, is reflected in the receiving bodies of water and resident organisms at all trophic levels. The use of $\delta^{15}N$ therefore allows the detection and relative quantification of sewage-derived nutrient enrichment in aquatic food webs (Cabana & Rasmussen 1996; McClelland *et al.* 1997; Udy *et al.* 1999). We have therefore used the $\delta^{15}N$ signal of important, long-lived and ubiquitous primary consumers (e.g. *Pinna carnea, Lytechinus variegates*) to establish our gradient of nutrient enrichment disturbance across sites in Barbados, Dominican Republic and Panama (Table 1) where we examined attributes of seagrass communities and food webs. Human population densities, correlated with $\delta^{15}N$ signals, were calculated using watershed areas and human population from the best available topographic and population maps as well government census data. These relationships were tested for significance using statistical components of Sigmaplot (version 7.0, SPSS Inc., 2001).

Tissue samples of invertebrates were collected during transect surveys. Muscle tissue was sampled from molluscs. Test and test linings were sampled from echinoids and arms tips from asteroids. All samples were dried for 24hrs at 80° C. Samples were then acid-washed (24 hrs in 10% HCl) to remove carbonates that could potential affect δ^{13}C values to be used in other studies (Tewfik et al., unpublished), dried for another 24 hrs at 80° C, ground to a fine powder and packed into 4 mm x 6 mm tin capsules. Stable isotope analyses were performed on a mass spectrometer at the G.G. Hatch laboratories, Department of Earth Sciences, University of Ottawa. Replicate samples (N=24) showed good technical precision for δ^{15}N signals (SD=0.19 ‰).

Community structure across the gradient

Macrophyte biomass and mega-invertebrate density surveys were conducted using transects and quadrats in 11 distinct seagrass beds in Barbados (N=1), Dominican Republic (N=7) and Panama (N=3) (Table 1). Seagrass beds were selected to reduce the influence of acute physical disturbance (i.e. wave energies) by avoiding the three highest wave exposure categories according to definitions by (Hiscock 1996.) Standardized, 60 x 3 metre, transects, two to six per site, were conducted using SCUBA or snorkel within the seagrass beds in two to seven metres depth. Macrophyte biomass and associated detritus was measured within 0.25 X 0.25 m quadrats placed at 20, 40 and 60 m along each transect. All aboveground detritus (up to 1 cm^2) and living macrophytes (seagrass: *Thalassia*; *Syringodium* and macroalgae: e.g. *Halimeda; Penicillus; Avrainvillea*) were collected, separated, dried for approximately 24 hours at 80° C, weighed (± 0.01 g), and finally converted to grams dry weight per square metre and percent biomass. Only a visual assessment was used for macrophyte and detritus values at B1 due to rough sea conditions.

Mega-invertebrate densities were determined, within the transect area of 180 m^2, by carefully searching through macrophytes, identifying all large invertebrate animals encountered on and partially in the sediment and expressing as the number of individuals per hectare. Tissue samples were extracted from some individuals for isotopic analysis. A diversity index was also calculated using the Shannon-Weiner method which combines presence/absence and proportional abundance of a species to give a community index. Consumer functional groups were established as follows: a) epiphyte/detritus specialists (*Strombus gigas, S. costatus, S. raninus, S. pugilus*); b) generalists (*Lytechinus variegates, Tripneustes ventricosus, Diadema antillarium,*); c) sub-surface deposit feeders (*Meoma venrticosa*, sand dollars); d) surface deposit feeders (*Oreaster reticulatus,* sea cucumbers) and e) suspension feeders (*Pinna carnea, Cassiopea spp.*). Although some invertebrate predators/scavengers (*Murex spp, Pleuroploca gigantean, Cassis spp.*) were encountered and included in the calculation of diversity, low densities precluded the construction of useful patterns of distribution across the nutrient gradient.

Regressions & Model fitting

All regressions of resources and consumers, including consumer abundance and diversity, were made across the gradient of increasing nutrient enrichment established from δ^{15}N values of consumers as a function of human population density. Regressions were made using acrsine square root transformed percentages of resource biomass (gDW/m^2) and consumer density (indv./ha) as well as log transformed resource biomass (gDW/m^2) and consumer density (indv./ha). This "double" analysis was undertaken in order to address the potential problems of constraints in the covariance and correlation structure and subsequent interpretation linked to the use of compositional data (Jackson 1997). However, given the fact that similar patterns were established using both types of data "...it is of little consequence which form of data is chosen" (Jackson 1997). Therefore, only the compositional data will be presented. Again, statistical evaluations of regressions were made using Sigmaplot (version 7.0, SPSS Inc., 2001). Due to the fact that many of our regressions showed potential for parabolic behaviour we fit all regressions using linear and quadratic equations and then employed a χ^2 test of significance of the quadratic term. These statistical evaluations were done using programs created in the statistical package, R (version 1.9.0, The R Development Core Team, 2004) the significant ($P < 0.05$) results of which are presented as part of the figure captions.

Results

Nutrient Enrichment gradient

What is clear from Fig. 1 is that a substantial (≈ 3.4 ‰, a full trophic level) and significant ($P<0.0001$) increase in $\delta^{15}N$ occurs within tissues of benthic organisms (using the suspension feeder *Pinna carnea* as a practical indicator) living in seagrass ecosystems over greater than three orders of magnitude increases in human population density within watersheds. This strong positive relationship also holds true for a number of other primary consumers including: the specialist *Strombus gigas* ($R^2 = 0.82$, $P = 0.0008$); the generalist *Lytechinus variegatus* ($R^2 = 0.73$, $P = 0.0004$); and the deposit feeder *Oreaster reticulatus* ($R^2 = 0.83$, $P = 0.0002$). This likely reflects the high levels of urban organic pollution being delivered to adjacent nearshore zones and resident organisms and is in good agreement with previous studies (Cabana & Rasmussen 1996; McClelland *et al.* 1997; Udy *et al.* 1999). Hence, perhaps not surprisingly, high human densities are strongly correlated to high levels of nutrient enrichment.

Community structure across the gradient

At the broadest level, fairly distinct patterns emerge amongst mega-invertebrate density and diversity across the nutrient enrichment gradient. First, an obvious and dramatic increase in total mega-invertebrate consumer density (individuals/hectare) is apparent (Fig 2a). These densities are extordinarily high, peaking at over 163 000 individuals per hectare, and comparable to other examples of runaway consumers studied in the literature (Rose *et al.* 1999; Jefferies 2000). Such high grazer densities are accompanied by a simultaneous strong decrease in the overall diversity of mega-invertebrate consumers which reaches its maximum at low to intermediate consumer densities (Fig. 2b).

To further explore this interesting pattern we examine the detailed distribution of both the resource community composition (benthic producers) (Fig. 3) and the consumer community composition (Fig. 4) across our disturbance gradient. We begin to see specific functional groups and associated life history strategies predominate. At low nutrient enrichment levels secondarily colonizing *Syringodium* are mixed with the "climax" seagrass *Thalassia* and associated detritus (Fig. 3). Additionally, a distinct peak in macroalgae biomass occurs at intermediate levels of nutrients (Fig 3d).

Interestingly, the increase in consumer abundance is accompanied by a dramatic decrease in detritus (positively correlated, $y = 32.5\ x + 17.9$, $R^2 = 0.16$, $P = 0.007$, over the nutrient enrichment spectrum) and *Syringodium* (Fig. 3a,b) while *Thalassia,* known to be less edible (Cebrian 1998), was found to increase significantly (Fig. 3c). These results suggest a compensatory response by *Thalassia* to the increased top-down consumptive pressure on *Syringodium* and detritus induced by the tremendously high density of generalist consumers.

The consumer pattern superimposed on that of the producers finds competitive specialist grazers (i.e. *Strombus spp.*) appearing to decline dramatically while generalist consumers increase (Fig. 4a,b). Thus, the pattern of increasing consumer abundance appears to be driven by the rise in generalist consumers (i.e. *Lytechinus variegatus*). This is intriguing in light of the gradient of nutrient enrichment and suggests that generalist consumers may be better able to utilize alternative resources (i.e. opportunistic autotrophs) that increase production in the anthropogenic induced, eutrophic environment. Further, as nutrient inputs increase and detritus is lost sub-surface deposit feeders (e.g. *Meoma ventricosa*) (Fig 4c) decline significantly while both surface deposit feeders (e.g. *Holothuria mexicana*) (Fig. 4d) and suspension feeders (*Pinna carnea, Cassieopia spp.*) (Fig. 4e) first increase, reaching their peaks at intermediate nutrient levels, before decreasing when nutrient enrichment is high and opportunistic generalist echinoid (i.e. *Lytechinus variegates, Tripneustes ventricosus*) consumer abundance is at extraordinarily high levels (>66,000/ha). Such consumers are characterized by an ability to feed on resources in the water column or immediately in contact with the water column (surface sediments). Such a pattern may suggest that some of the nutrient enrichment is being manifested as phytoplanktonic production and it's accompanying phytoplankton detritus

Discussion

Given the increasing levels of anthropogenic disturbance occurring in all ecosystems it is prudent to begin examining similar systems across a gradient of such change. Such empirical analysis may contribute to our understanding of food web structure and function as we start the difficult task of amelioration and restoration of disturbed habitats which may have already moved toward alternate states that may be persistent (Sousa 2000). Here, we explored the influence of nutrient enrichment, which appears to significantly increase with human population density, across a number of Caribbean seagrass communities.

Density, Diversity and Detritus

As we view patterns of mega-invertebrate abundance (density) and diversity across our gradient we see that they are generally in agreement with empirical models, based on temperate marine systems, for the succession of macro-fauna as a function of organic enrichment (Pearson & Rosenberg 1978). The distinct peaks of these patterns occur in very different places along the gradient and again reflect known general patterns of diversity (intermediate disturbance hypothesis, (Huston 1979), and abundance (increasing opportunists, (Grall & Chauvaud 2002; Peterson *et al.* 2002) in other studies. Along the latter portion of this enrichment gradient we find a dramatic decrease in mega-invertebrate diversity accompanied by a similar dramatic decrease in detrital biomass. Although only a correlation, it does suggest that detrital dynamics may be playing a fundamental role in the maintenance of diversity in these ecosystems and deserves experimental consideration (Tewfik et al., submitted)

It is reasonably well established that living seagrass tissue is not readily consumed by many herbivores, although exceptions exist (Valentine & Heck 1999), and that the bulk of organic transfer in seagrass meadows to higher trophic levels is via the detrital pathway (Stoner *et al.* 1995; Pomeroy 2001; Vizzini *et al.* 2002). The importance and preference of macro (Vadas *et al.* 1982; Stoner *et al.* 1995), particulate (Regis 1986) and re-suspended (Kennedy *et al.* 2001) detritus to a wide variety of primary consumers in seagrass communities substantiates the important link between diversity and detritus (Moore *et al.* 2004).

Functional Groups across the Gradient

The emerging patterns also suggest that distinct or suites of functional groups and associated life histories, at both the producer and primary consumer levels predominate at distinct ranges of anthropogenic nutrient enrichment. The relatively high diversity of mega-invertebrates at the lower end of the nutrient enrichment spectrum, specifically specialists, is thought to be strongly linked to a diversity of resources including various forms (benthic, resuspended) of living and detrital seagrass, epiphytes etc. This is perhaps most relevant to the physical and chemical diversity of substrates entering the detrital pool and sets the stage for the evolution and maintenance of detritivore diversity (Moore *et al.* 2004). This increased detritivore diversity in turn impacts nutrient recycling rates thereby accentuating overall diversity within the system.

As nutrient enrichment increases secondary colonizing seagrasses (*Syringodium*) are out competed by climax species (*Thalassia*) (Williams 1990). Although no significant change in absolute *Thalassia* biomass is apparent (only example where absolute biomass data as a function of nutrient enrichment did not conform to percentage data), the loss of *Syringodium* begins to narrow the scope of producer diversity and may also begin to impact on the variety of detritus within the traditional autochthonous pool. The emergence of macroalgae at intermediate nutrient enrichment may be linked to their partial release from nutrient competition with seagrasses in the classic successional sequence (Williams 1990). It may also be associated to the transitory decline in generalists that may graze on them and the dominance by surface deposit and suspension feeding consumers, which would not directly consume macroalgae, and may themselves be responding to elevated levels of living and detrital sources of phytoplankton and epiphytic detritus due to increasing nutrient loading (Cloern 2001). At high, chronic levels of nutrient loading water quality may be severely impacted with decreased levels of light and oxygen as well as accretion of sediments (Grall & Chauvaud 2002) creating ambient conditions that only the most stress tolerant/competitive producers (i.e. *Thalassia*) and generalist consumers (i.e. echinoids) may survive.

Maintenance of Diversity

The reasons for the maintenance of high diversity in and of itself at the low to intermediate levels of nutrient enrichment are generally thought to be three-fold. Firstly, the low palatability of the primary producers generating the majority of the detritus (i.e. *Thalassia*) (Tribble 1981; Cebrian 1998) largely guarantees the existence of a autochthonous detrital pool. Secondly, the interdependent processing chain concerned with the physical and chemical breakdown of detritus increases the number of functional groups and total species involved in the detrital pathway (Moore *et al.* 2004). Finally, the relative densities of primary consumers, including those capable of direct producer consumption (i.e. urchins), are controlled through competition, predation and intra-guild predation so as to avoid run away consumption of any particular species or functional group (Polis *et al.* 1989; Polis & Strong 1996). The persistence of the detrital pool benefits many organisms both as a nutritious food source (detritus and associated microbial, fungal, and metazoan film) as well as shelter provided for all life histories stages including the extremely vulnerable post-planktonic larvae. It is perhaps then not surprising that with the loss of detritus we also see a loss in diversity.

Towards Food Web Simplification

Increasing nutrient enrichment is thought to facilitate stress-tolerant/competitive benthic producers (*Thalassia* vs. *Syringodium*) (Grime 1977; Williams 1990) as well as begin the switch to pelagic (i.e. phytoplankton) production which results in light limitations and sediment accretion (Short & Wyllie-Echeverria 1996; Grall & Chauvaud 2002). The decrease in traditional benthic production, and associated detritus, and the increased availability of opportunistic phytoplankton and associated dertitus as well as epiphytes may allow the increase in surface deposit, suspension (both in a transitory manner) and most importantly generalist consumer populations. The use of such alternate resources by these functional groups has been previously documented (Lawrence 1975; Harmelin *et al.* 1981; Regis 1986; Polis & Strong 1996; Iken *et al.* 2001). Also, the importance of specific resources to various functional groups has been previously observed with higher condition factors for conch and urchins with increasing levels of detritus and *Syringodium* respectively (Tewfik et al. unpublished data). However, the more generalized palette (Tewfik et al. unpublished data) and morphological plasticity of urchins (Regis 1986) allows survival across a much wider gradient of environmental parameters even in the absence of presumably preferred, traditional resources.

Conclusions

Seagrass food webs impacted by high nutrient enrichment show substantial simplification with considerably reduced producer and consumer diversity but extremely high numbers of generalist consumers (i.e. urchins) that may be strongly subsidized indirectly through high levels of nutrients to alternate resources including phytoplankton and associated detritus and opportunistic epiphytes (Fig. 5). These high numbers of generalists may severely restrain recovery of diversity, even when nutrient enrichment is alleviated, as they strongly suppress both benthic producers and competitive consumers through grazing and intra-guild predation (Fig. 5). Although overgrazing and deforestation of macrophyte dominated systems (e.g. California, Mediterranean, Eastern Canada) has largely been attributed to predator and competition release of urchins due to overfishing the contribution and potential significance of nutrient enrichment should not be ignored (Sala *et al.* 1998; Steneck *et al.* 2002)

The importance and utility of including donor-controlled alternate resources and pathways, including allochthonous inputs (e.g. nutrients, phytoplankton detritus), into food web dynamics has been highlighted in a number of recent papers (Polis & Strong 1996; Polis *et al.* 1997; Huxel & McCann 1998; Jefferies 2000;

Huxel *et al.* 2002; Moore *et al.* 2004; Schindler & Lubetkin 2004). Such subsidies have been documented via a number of different pathways in a variety of different systems: macroalgal detritus to desert islands (Polis *et al.* 1997) and submarine canyons (Vetter & Dayton 1999); phytoplankton detritus to abyssal plains (Iken *et al.* 2001); guano and carrion at seabird nesting sites (Sanchez-Pinero & Polis 2000); and agricultural production and fertilizers to migrating waterfowl (Jefferies 2000). These subsidies have been shown to greatly increase the number of consumers which ultimately depress in situ resources. However, due to the allochthonous nature (i.e. donor-controlled) of the subsidy such systems can remain stable (Huxel & McCann 1998) even as complexity is lost and a single, large flow of energy eventually dominates the system. We have proposed such a dynamic in highly nutrient enriched seagrass beds (Fig. 5b) where generalist urchins compose the majority of consumer abundance (>98%) and where traditional seagrass derived detrital pathways have been largely eliminated resulting in low diversity throughout the community.

The long-term sustainability of simplified foodwebs ("alternate states"), the loss of significant production and ecosystem services, and resultant impacts on other interconnected systems (i.e. seagrass-coral reef-mangrove habitat complex) should be at the heart of future research agendas. What is equally important is whether we can work our way back from these potentially altered states and the development of specific tools and techniques to bring about such a fundamental changes. These questions relate directly to the rebuilding of renewable resource bases and the reasonably intact and diverse systems from which we derive them. Ultimately, we feel the examination of change within food webs goes to the heart of studies in ecology especially when one considers the extent to which nutrient loading and fisheries exploitation (synergistic effects, see figure 3 in (Jackson *et al.* 2001) have already affected the ecology of coastal systems globally.

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Literature Cited

Cabana G. & Rasmussen J.B. (1996) Comparison of aquatic food chains using nitrogen isotopes. *Proceedings of the National Academy of Science of the United States of America*, 93, 10844-10847

Camp D.K., Cobb S.P. & van Breddveld J.F. (1973) Overgrazing of grasses by a regular urchin, *Lytechinus variegatus*. *Bioscience*, 23, 37-38

Carpenter S., Ludwig D. & Brock W. (1999) Management of eurtrophication for lakes subject to potentially irreversible change. *Ecological Applications*, 9, 751-771

Cebrian J.D., C.M. (1998) Patterns in leaf herbivory on seagrass. *Aquatic Botany*, 60, 67-82

Cloern J.E. (2001) Our evolving conceptual model of the coastal eutrophication problem. *Marine Ecology Progress Series*, 210, 223-253

Cohen J., Briand F. & Newman C. (1990) *Community Food Webs: Data and Theory*. Springer-Verlag, Heidelberg & New York.

DeAngelis D. (1992) *Dynamics of Nutrient Cycling and Food Webs.* Chapman and Hall, London.

Duarte C.M. (1995) Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia*, 41, 87-112

Grall J. & Chauvaud L. (2002) Marine eutrophication and benthos: the need for new approaches and concepts. *Global Change Biology*, 8, 813-830

Grime J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist*, 111, 1169-1194

Harmelin J., Bouchon C. & Hong J. (1981) Impact de la pollution sur la distribution des echinodermes des substrats durs en provence (Mediterranee Nord-Occidentale). *Tethys*, 10, 13-36

Hiscock K. (1996.) *Marine Nature Conservation Review: Rationale and methods.* Nature Conservancy Council, Peterborough.

Hobson K.A. & Welch H.E. (1992) Determination of trophic relationships within high Arctic marine food webs using 13C and 15N analysis. *Marine Ecology Progress Series*, 84, 9-18

Hughes T. (1994) Catastrophes, Phase shifts, and large-scale degredation of Caribbean coral reefs. *Science*, 265, 1547-1551

Huston M. (1979) A general hypothesis of species diversity. *American Naturalist*, 113, 81-101

Huxel G.R. & McCann K.S. (1998) Food web stability: The influence of trophic flows across habitats. *American Naturalist*, 152, 460-469

Huxel G.R., McCann K.S. & Polis G.A. (2002) Effects of partitioning allochthonous and autochthonous resources on food web stability. *Ecological Research*, 17, 419-432

Iken K., Brey T., Wand U., Voigt J. & Junghans P. (2001) Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. *Progress in Oceanography*, 50, 383-405

Jackson D.A. (1997) Compositional data in community ecology: the paradigm or peril of proportions. *Ecology*, 78, 929-940

Jackson J.B.C. (2001) What was natural in the coastal oceans? *Proceedings of the National Academy of Science of the United States of America*, 98, 5411-5418

Jackson J.B.C., Kirby M.X., Berger W.H., Bjorndal K.A., Botsford L.W., B.J. B., Bradbury R.H., Cooke R., Erlandson J., Estes J.A., Hughes T.P., Kidwell S., Lange C.B., Lenihan H.S., Pandolfi J.M., Peterson C.H., Steneck R.S., Tegner M.J. & Warner R.R. (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 293, 629-638

Jefferies R. (2000) Allochthonous inputs: integrating population changes and food-web dynamics. *Trends in Ecology and Evolution*, 15, 19-22

Kennedy H., Richardson C.A., Duarte C.M. & Kenedy D.P. (2001) Diet and association of *Pontonia pinnphylax* occuring in *Pinna nobilis:* insights from stable isotope analysis. *Journal of the Marine Biological Association of the United Kingdom*, 81, 177-178

Lawrence J. (1975) On the relationship between marine plants and sea urchins. *Oceanography and Marine Biology: An Annual Review*, 13, 213-286

Martinez N. (1991) Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. *Ecological Monographs*, 61, 367-392

McClelland J.W., Valiela I. & Michener R.H. (1997) Nitrogen-stable isotope signatures in esturine food webs: A record of increasing urbanization in coastal watersheds. *Limnology and Oceanography*, 42, 930-937

Moore J., Berlow E., Coleman D., de Ruiter P., Dong Q., Hastings A., Collins-Johnson N., McCann K., Melville K., Morin P., Nadelhoffer K., Rosmond A., Post D., Sabo J., Scow K., Vanni M. & Wall D. (2004) Detritus, Trophic Dynamics, and Biodiversity. *Ecology Letters*, 7, 584-600

Pearson T. & Rosenberg R. (1978) Macrobenthic successions in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology: An Annual Review*, 16, 229-311

Peterson B.J. & Fry B. (1987) Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics*, 18, 293-320

Peterson B.J., Rose C.D., Rutten L.M. & Fourqurean J.W. (2002) Disturbance and recovery following catastrophic grazing: studies of successional chronosequence in a seagrass bed. *Oikos*, 97, 361-370

Polis G.A., Anderson W.B. & Holt R.D. (1997) Toward an integration of landscape and food web ecology. *Annual Review of Ecology and Systematics*, 28, 289-316

Polis G.A., Myers C.A. & Holt R.D. (1989) The ecology and evolution of intraguild predation: Potential competitors that eat each other. *Annual Review of Ecology and Systematics*, 20, 297-330

Polis G.A. & Strong D.R. (1996) Food web complexity and community dynamics. *American Naturalist*, 147, 813-846

Pomeroy L. (2001) Caught in the food web: complexity made simple? *Scientia Marina*, 65, 31-40

Regis M. (1986) Microstructure adaptive des radioles de *Paracentrotus lividus* (Echinodermata: Echinoidea) en milieu eutrophise par des eaux usees. *Marine Biology*, 90, 271-277

Rose C.D., Sharp W.C., Kenworthy W.J., Hunt J.H., Lyons W., G,, Prager E.J., Valentine J.F., Hall M.O., Whitfield P.E. & Fourqurean J.W. (1999) Overgrazing of a large seagrass bed by the sea urchin *Lytechinus variegatus* in Outer Florida Bay. *Marine Ecology Progress Series*, 190, 211-222

Sala E., Boudouresque C.F. & Harmelin-Vivien M. (1998) Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. *Oikos*, 82, 425-439

Sanchez-Pinero F. & Polis G.A. (2000) Bottom-up dynamics of allochthonous input: Direct and indirect effects of seabirds on islands. *Ecology*, 81, 3117-3132

Scheffer M., Carpenter S., Foley J.A., Folke C. & Walker B. (2001) Catastrophic shifts in ecosystems. *Nature*, 413, 591-596

Scheffer M., Hosper S., Meijer M.-L., Moss B. & Jeppesen E. (1993) Alternative equilibria in shallow lakes. *Trends in Ecology and Evolution*, 8, 275-279

Schindler D. & Lubetkin S. (2004) Using sable isotopes to quantify material transport in food webs. In: *Food webs at the landscape level* (eds. Polis G, Power M & Huxel G), pp. 25-42. The University of Chicago Press, Chicago

Short F.T. & Wyllie-Echeverria S. (1996) Natural and human-induced disturbance of seagrasses. *Environmental Conservation*, 23, 17-27

Sousa W.P. (2000) Natural disturbance and the dynamics of marine benthic communities. In: *Marine Community Ecology* (eds. Bertresss MD, Gaines SD & Hay ME), pp. 85-130. Sinauser Associates

Steneck R.S., Graham M., Bourque B., Corbett D., Erlandson J., Estes J. & Tegner M. (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental Conservation*, 29, 436-459

Stoner A.W., Ray M. & Waite J.M. (1995) Effects of a large herbivorous gastropod on macrofauna communities in tropcal seagrass meadows. *Marine Ecology Progress Series*, 121, 125-137

Tribble G.W. (1981) Reef-based herbivores and the distribution of two seagrasses (*Syringodium filiforme* and *Thalassia testudinum*) in the San Blas Islands (Western Caribbean). *Marine Biology*, 65, 277-281

Udy J.W., Dennison W.C., Long W.J.L. & McKenzie L.J. (1999) Responses of seagrass to nutrients in the Great Barrier Reef, Australia. *Marine Ecology Progress Series*, 185, 257-271

Vadas R.L., Fenchel T. & Ogden J.C. (1982) Ecological studies of the sea urchin, *Lytechinus variegatus*, and the algal-seagrass communities of the Miskito Cays, Nicaragua. *Aquatic Botany*, 14, 109-125

Valentine J.F. & Heck K.L. (1991) The role of sea urchin herbivory 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

Valentine J.F. & Heck K.L. (1999) Seagrass herbivory: Evidence for continued grazing of marine grasses. *Marine Ecology Progress Series*, 176, 291-302

Vetter E. & Dayton P. (1999) Organic enrichment by macrophyte detritus and abundance patterns of megafaunal populations in submarine canyons. *Marine Ecology Progress Series*, 186, 137-148

Vizzini S., Sara G., Michener R.H. & Mazzola A. (2002) The role and contribution of seagrass *Posidonia oceanica* (L.) Delile organic matter for secondary consumers as revealed by carbon and nitrogen stable isotope analysis. *Acta Oecologica*, 23, 277-285

Williams S.L. (1990) Experimental studies of Caribbean seagrass bed development. *Ecological Monographs*, 60, 449-469

Tables

Table 1: Description of seagrass sites including levels of nutrient loading (based on $\delta^{15}N$, Fig. 1) and general description of watershed.

Site location	Site Code	Nutrient loading	Watershed description
Punta Chimanche, Pedernales, Dom. Rep.	DR7	zero	wilderness
Baie Rousel, Pedernales, Dom. Rep.	DR5	zero	wilderness
Bahia de las Aguilas, Pedernales Dom. Rep.	DR4	zero	wilderness
Puerto de la Alcoa (outer marker), Dom. Rep	DR6	low	wilderness
Puerto de la Alcoa (dock, south), Dom. Rep	DR3	low	rural
Puerto de la Alcoa (dock, north), Dom. Rep	DR2	low	rural
Solarte Sur, Bocas del Toro, Panama	P3	moderate	rural
Bastimentos mangroves, Bocas del Toro, Panama	P2	moderate	rural/wilderness
STRI dock, Bocas del Toro, Panama	P1	moderate	semi-urban
Barahona (inner harbour), Dom. Rep.	DR1	high	urban
St. Lawrence, South coast, Barbados	B1	high	urban

Figures

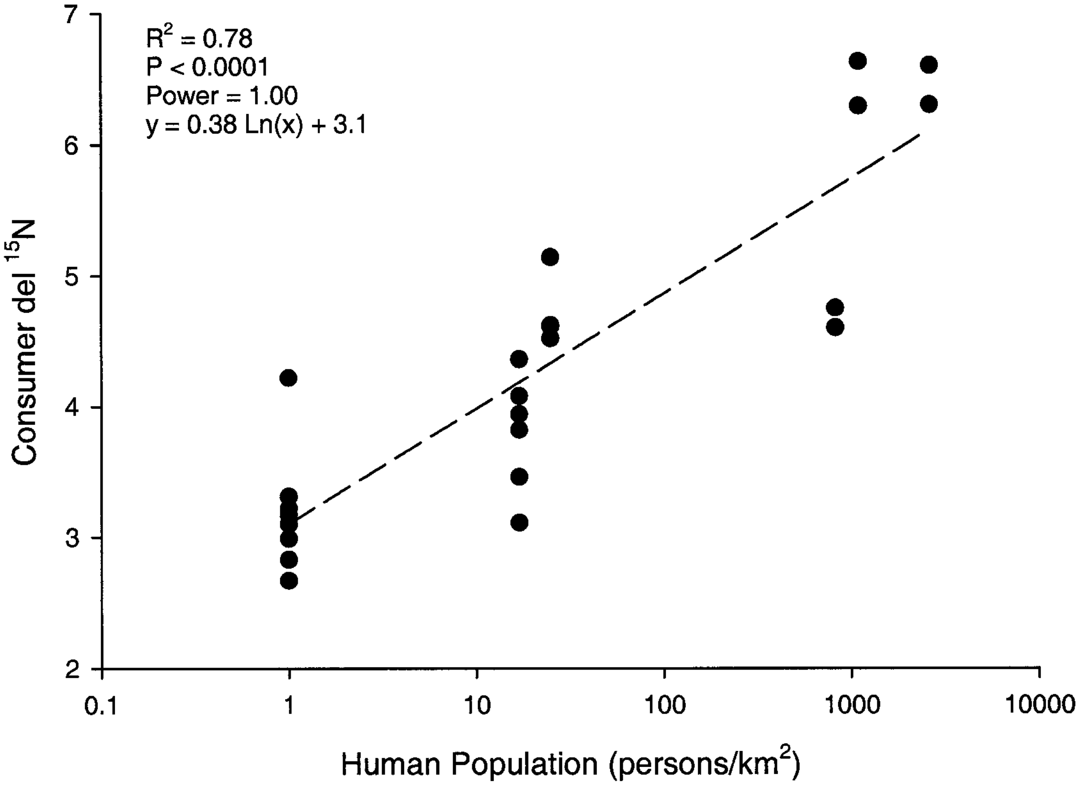

Fig. 1: Variation in $\delta^{15}N$ of primary consumers versus human population density (#/km^2) within watersheds (N=24). Watershed areas and human populations were calculated with the best available topographic and population maps as well government census data for Barabados, Dominican Republic and Panama. Consumers are represented by *Pinna carnea* except at site B1 where *Lytechinus variegates* was used in the absence of *P. carnea*. Correlation between *P. carnea* and *L. variegates* $\delta^{15}N$ values (N=14) across six sites was significant ($R^2 = 0.63$, $P < 0.0001$).

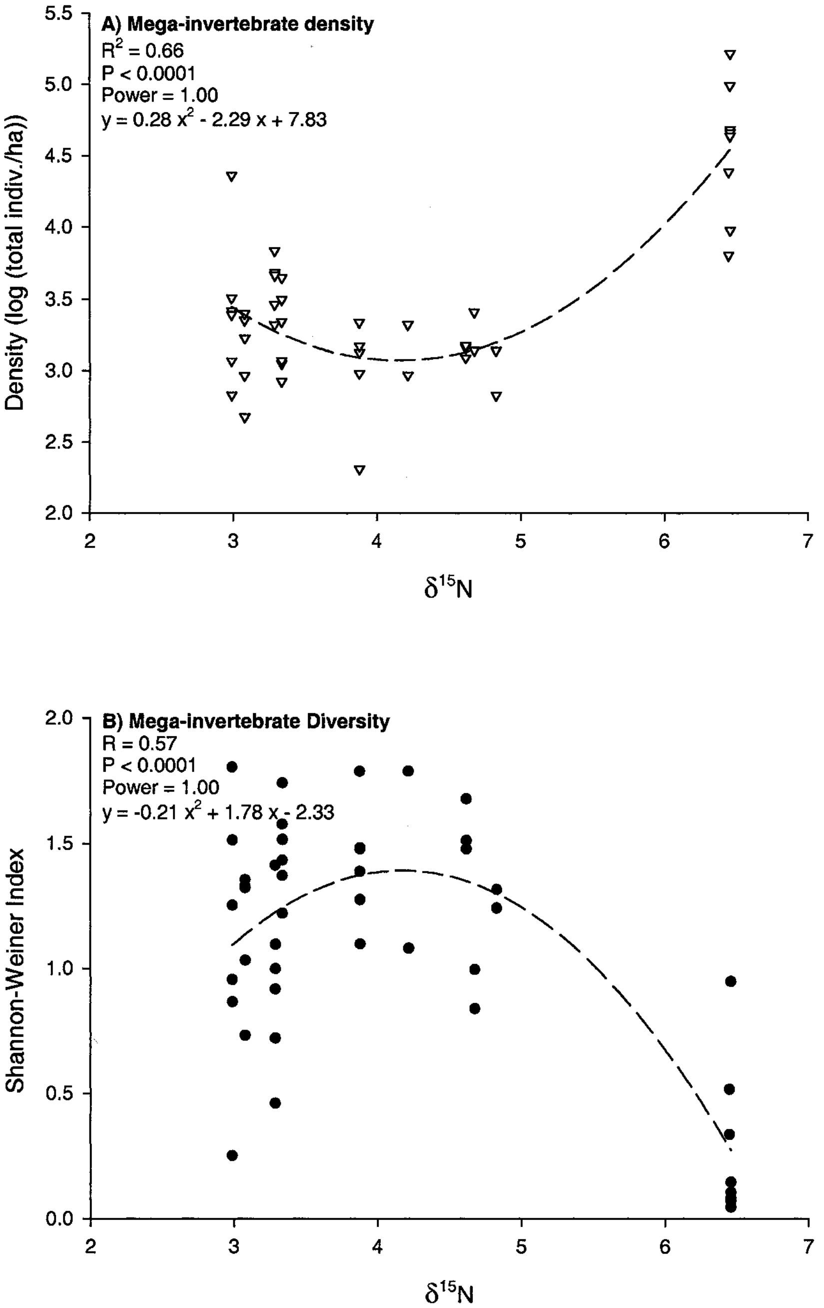

Fig 2: Relationships of (A) mega-invertebrate density (log of total individuals per hectare) and (B) diversity of mega-invertebrates (Shannon-Weiner index) along a nutrient loading gradient (based on $\delta^{15}N$, see Fig. 1) at 11 sites in Barbados, Dominican Republic and Panama (Table 1 for sites). (N=46). Quadratic fits were significant for (A) $\chi^2_{0.05,1} = 4.51$, $P < 0.0001$ and (B) $\chi^2_{0.05,1} = 2.69$, $P < 0.0001$

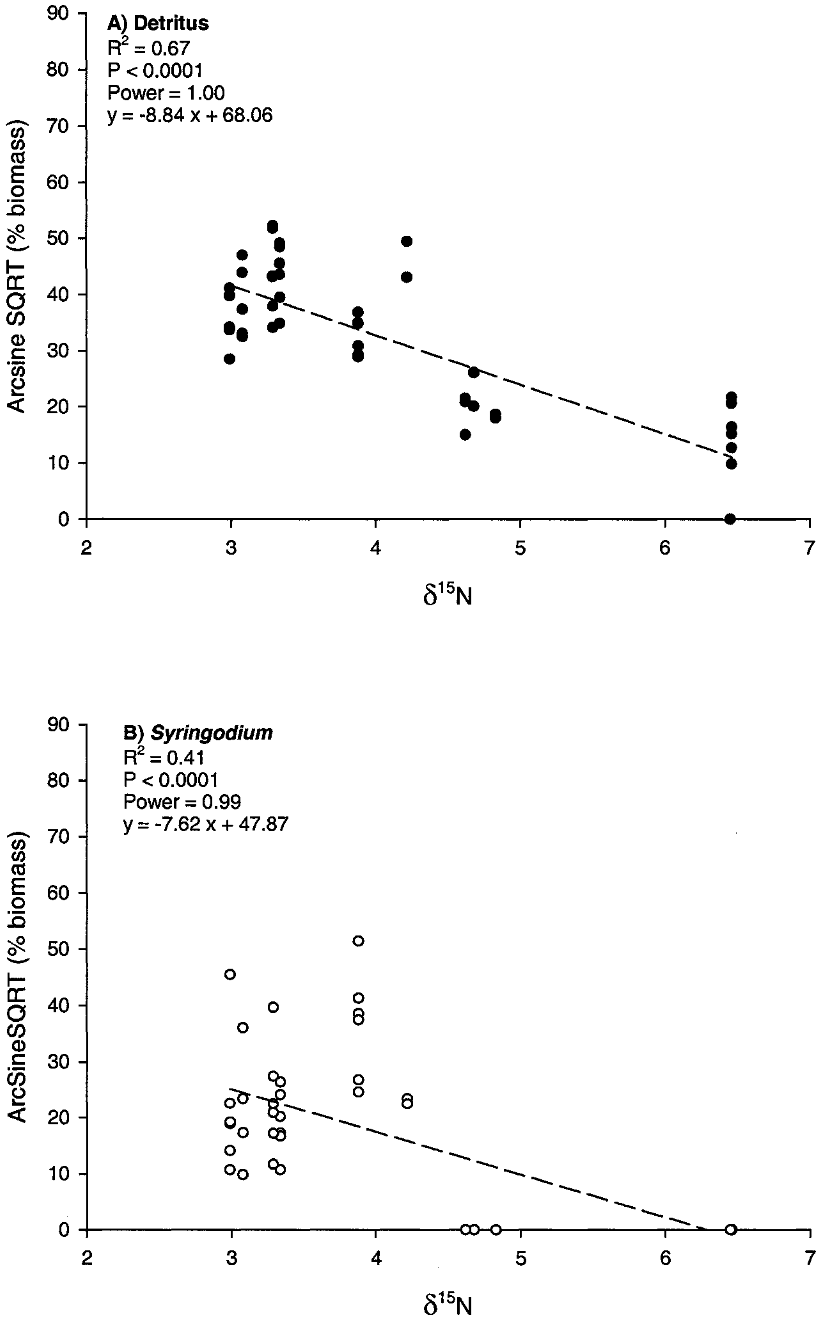

Fig 3: Percent biomass (gDW/m^2) of resources (Arcsine Square root transformed) along a gradient of increasing nutrient loading (based on $\delta^{15}N$, see Fig. 1) at sites in Barbados, Dominican Republic and Panama (Table 1 for sites). (N=46). (A) Detritus, (B) *Syringodium*, (C) *Thalassia*, (D) Macroalgae. Quadratic fits were significant for (D) $\chi^2_{0.05,1} = 1219$, $P < 0.0001$

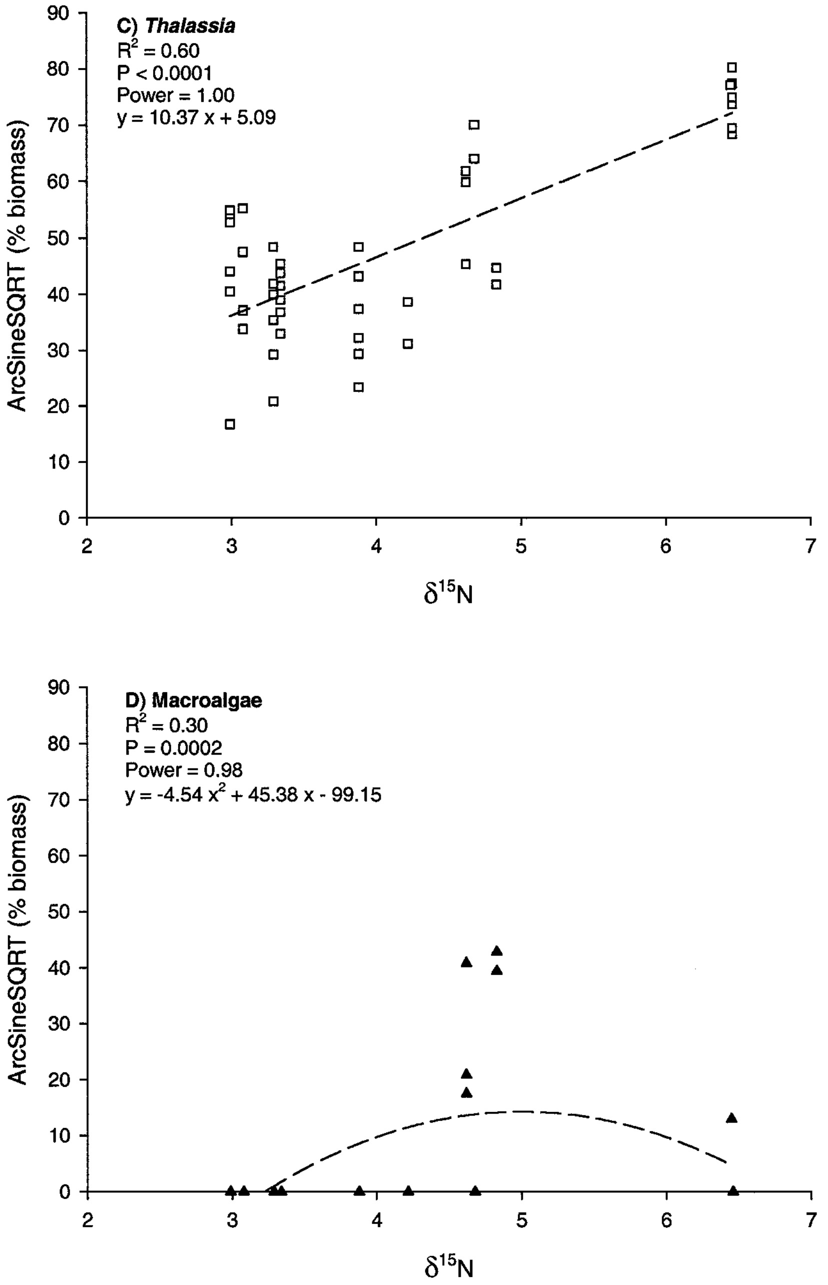

Fig 3 (continued): Percent biomass (gDW/m^2) of resources (Arcsine Square root transformed) along a gradient of increasing nutrient loading (based on $\delta^{15}N$, see Fig. 1) at sites in Barbados, Dominican Republic and Panama (Table 1 for sites). (N=46). A) Detritus, (B) *Syringodium*, (C) *Thalassia*, (D) Macroalgae. Quadratic fits were significant for (D) $\chi^2_{0.05,1} = 1219$, $P < 0.0001$

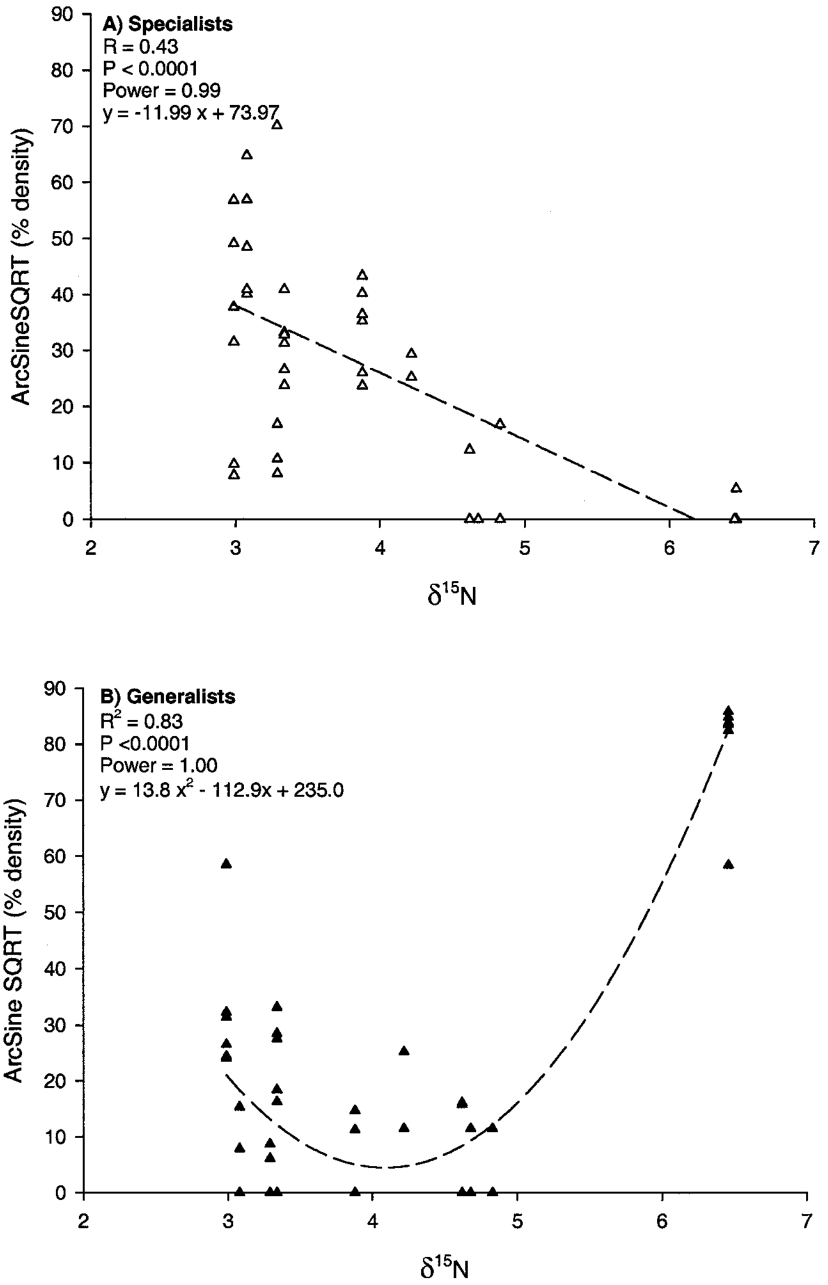

Fig. 4: Percent mega-invertebrate consumers (Arcsine Square root transformed % density) along a gradient of increasing nutrient loading (based on $\delta^{15}N$, see Fig. 1) at sites in Barbados, Dominican Republic and Panama (Table 1 for sites). (N=46). Consumer functional groups are as follows: A) Specialists (*Strombus gigas, S. costatus, S. raninus, S. pugilus*); B) Generalists (*Lytechinus variegates, Tripneustes ventricosus, Diadema antillarium*); C) Sub surface deposit feeders (*Meoma venrticosa*, sand dollars); D) Surface deposit feeders (*Oreaster reticulates*, sea cucumbers;) and E) Suspension feeders (*Pinna carnea, Cassiopea spp.*).Quadratic fits were significant for (B) $\chi^2_{0.05,\ 1} = 11294$, P< 0.0001, (D) $\chi^2_{0.05,\ 1} = 4565$, P< 0.0001 and (E) $\chi^2_{0.05,1} = 5803$, P< 0.0001.

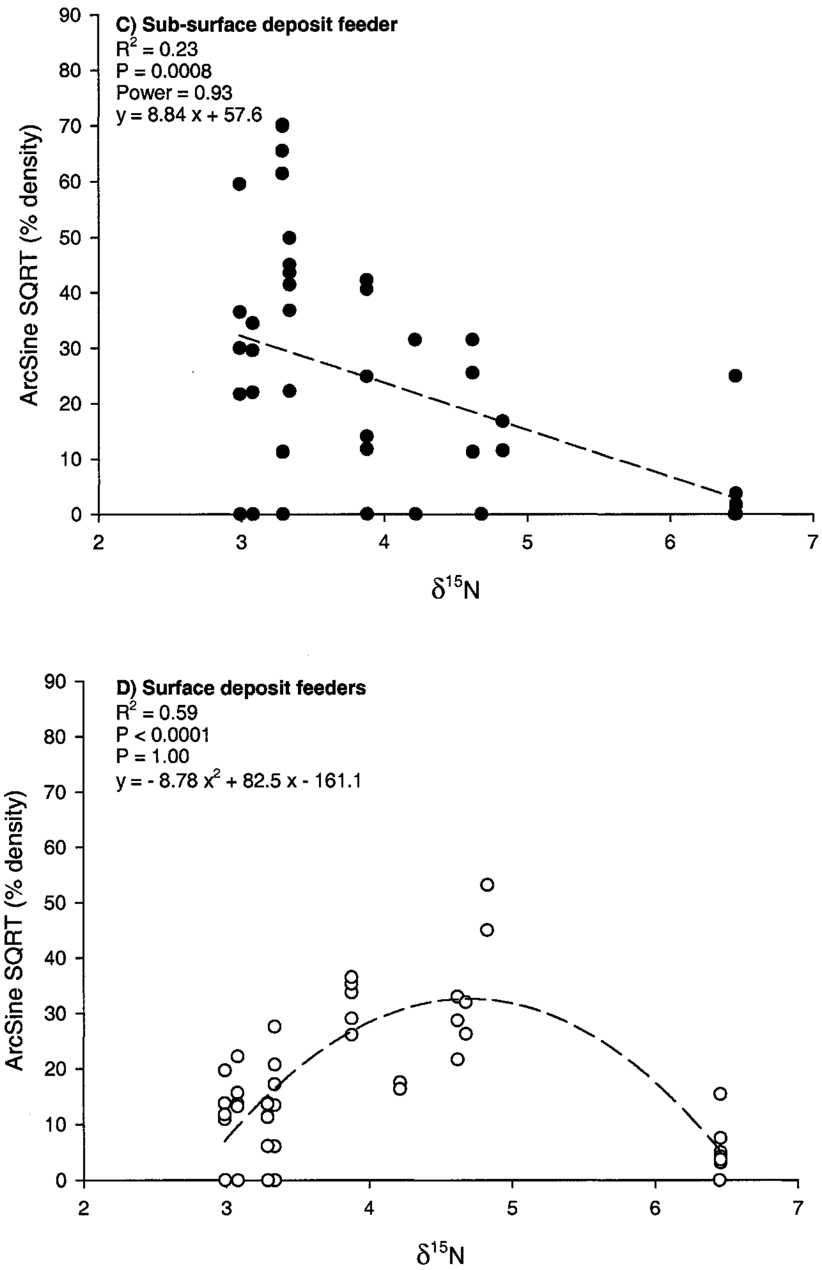

Fig. 4 (continued): Percent mega-invertebrate consumers (Arcsine Square root transformed % density) along a gradient of increasing nutrient loading (based on $\delta^{15}N$, see Fig. 1) at sites in Barbados, Dominican Republic and Panama (Table 1 for sites). (N=46). Consumer functional groups are as follows: A) Specialists (*Strombus gigas, S. costatus, S. raninus, S. pugilus*); B) Generalists (*Lytechinus variegates, Tripneustes ventricosus, Diadema antillarium*); C) Sub surface deposit feeders (*Meoma venrticosa*, sand dollars); D) Surface deposit feeders (*Oreaster reticulates*, sea cucumbers;) and E) Suspension feeders (*Pinna carnea, Cassiopea spp.*).Quadratic fits were significant for (B) $\chi^2_{0.05,1} = 11294$, P< 0.0001, (D) $\chi^2_{0.05,1} = 4565$, P< 0.0001 and (E) $\chi^2_{0.05,1} = 5803$, P< 0.0001.

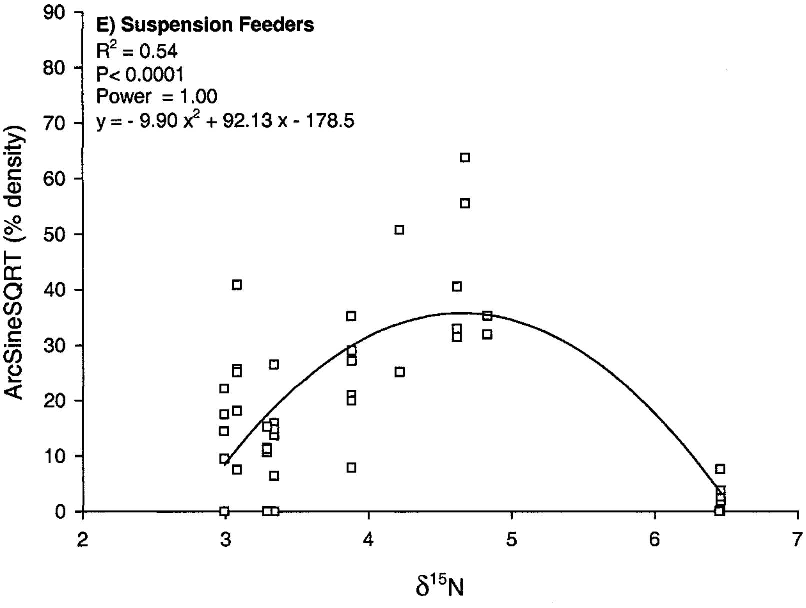

Fig. 4 (continued): Percent mega-invertebrate consumers (Arcsine Square root transformed % density) along a gradient of increasing nutrient loading (based on $\delta^{15}N$, see Fig. 1) at sites in Barbados, Dominican Republic and Panama (Table 1 for sites). (N=46). Consumer functional groups are as follows: A) Specialists (*Strombus gigas, S. costatus, S. raninus, S. pugilus*); B) Generalists (*Lytechinus variegates, Tripneustes ventricosus, Diadema antillarium*); C) Sub surface deposit feeders (*Meoma venrticosa*, sand dollars); D) Surface deposit feeders (*Oreaster reticulates,* sea cucumbers;) and E) Suspension feeders (*Pinna carnea, Cassiopea spp.*).Quadratic fits were significant for (B) $\chi^2_{0.05,1} = 11294$, P< 0.0001, (D) $\chi^2_{0.05,1} = 4565$, P< 0.0001 and (E) $\chi^2_{0.05,1} = 5803$, P< 0.0001.

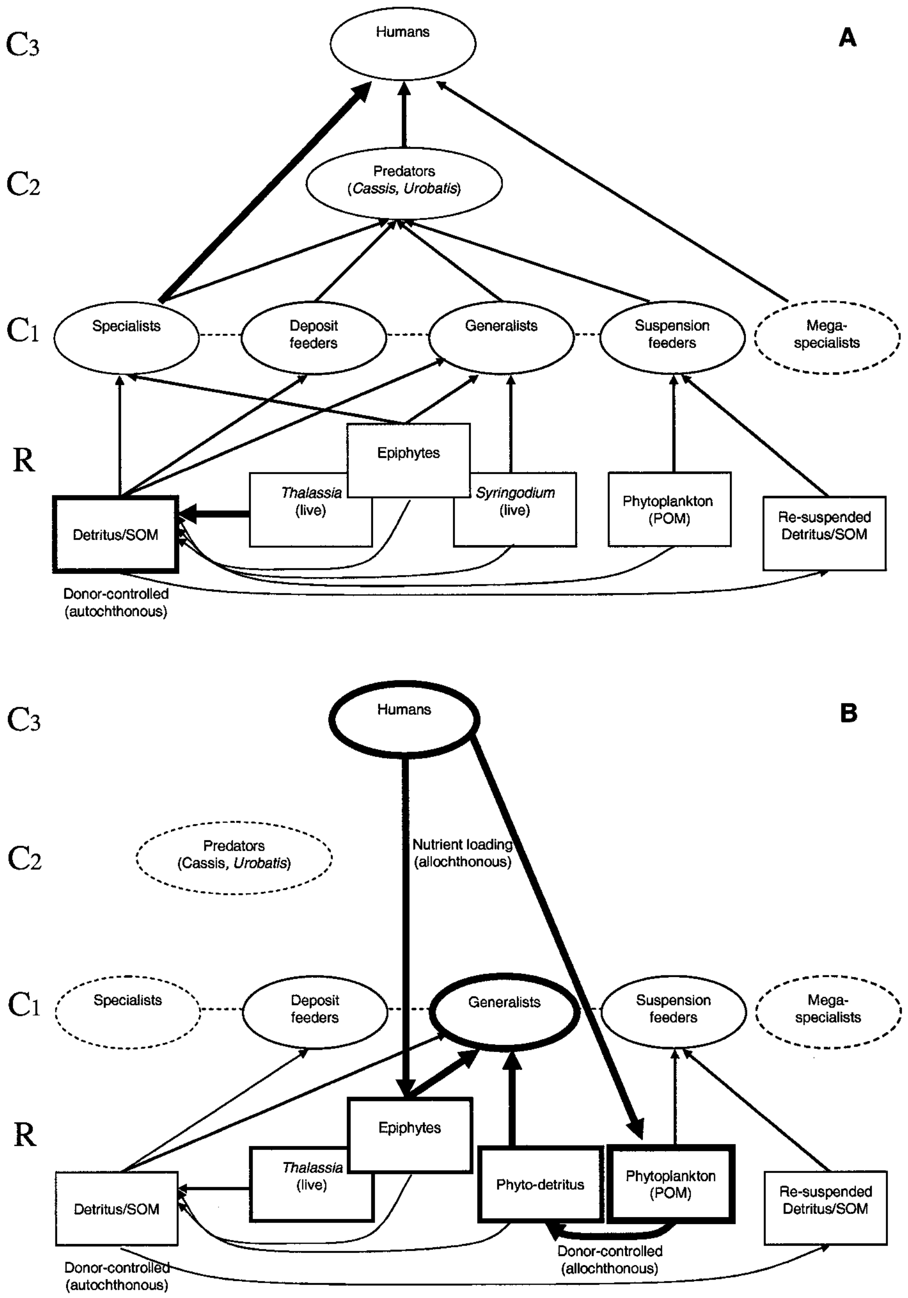
C3
Humans
A
C2
Predators
(*Cassis, Urobatis*)
C1
Specialists
Deposit feeders
Generalists
Suspension feeders
Mega-specialists
R
Epiphytes
Thalassia (live)
Syringodium (live)
Phytoplankton (POM)
Re-suspended Detritus/SOM
Detritus/SOM
Donor-controlled (autochthonous)
C3
Humans
B
C2
Predators
(Cassis, *Urobatis*)
Nutrient loading (allochthonous)
C1
Specialists
Deposit feeders
Generalists
Suspension feeders
Mega-specialists
R
Epiphytes
Thalassia (live)
Phyto-detritus
Phytoplankton (POM)
Re-suspended Detritus/SOM
Detritus/SOM
Donor-controlled (autochthonous)
Donor-controlled (allochthonous)

Fig. 5: Simplified schematics of Caribbean seagrass foodwebs after A) fishing and low nutrient loading and B) high levels of nutrient loading (fishing curtailed due to lack of targets and poor recruitment). Polygons, resources (R); ovals, consumers (C); arrows, energy flow. Weights of symbols indicate relative abundance (polygons, ovals) and flow (arrows). Mega–specialists: turtles, manatees; Specialists: conch (4 species); Surface deposit feeders: sea star, cucumbers; Sub-surface deposit feeders: heart urchin, sand dollars; Generalists: sea urchins; Suspension feeders: Bivalves (*Pinna*), jellyfish (benthic & pelagic); *Syringodium* more edible grass; epiphytes resident on seagrass leaves; Dotted line within trophic level represents competition, intra-guild predation.

Connecting Statement

In the preceding chapter, I explored the pattern of producer and consumer functional group across a wide and increasing gradient of nutrient loading. Nutrients facilitate stress tolerant/competitive benthic producers (*Thalassia* vs. *Syringodium*) as well as begin the switch to pelagic (i.e. phytoplankton) production which results in light limitations and sediment accretion. The decrease in traditional benthic production, and associated detritus, and the increased availability of opportunistic phytoplankton and associated phytoplankton dertitus as well as epiphytes may allow the increase in surface deposit, suspension (both in a transitory manner) and most importantly generalist consumer populations. This results in significant declines in the overall benthic producer and mega-invertebrate consumer diversity at the highest nutrient inputs. Allochthonous nutrients may ultimately allow drastic or "catastrophic" state shifts in the seagrass community due to the availability of "new" or expanded "subsidies" of allochthonous resources.

In the final chapter, I explore the source of the suspected resource "subsidy", described in chapter 2 and 3 using stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) within potential food resources and relating them to the values of consumer tissues and stomach contents. In general, food webs of the significantly nutrient enriched site have lighter (i.e. more negative) carbon values of primary consumers and higher nitrogen values overall. This indicates a potential switch to or subsidy from lighter resources such as epiphytes or phytoplankton and associated detritus within the ambient conditions of increased nitrogen availability (i.e. nutrient loading). The availability of such alternative resources to generalist urchins, in conjunction with other flexible life history traits, could potentially account for the existence of a drastically altered community where high densities of urchins continue to suppress "traditional" benthic macrophyte production through grazing and the recruitment of competitors and predators through intra-guild predation. The inclusion of such potential subsidies in community dynamics is critical especially in light of the interconnectedness of nature systems and the increasing influence of wide ranging anthropogenic disturbances in coastal systems globally.

Abstract

Overgrazing and deforestation of macrophyte dominated systems has often been linked to predator and competition release of urchins due to over-fishing. However, the contribution of nutrient loading to the progression and persistence of this phenomenon should also be considered. In an effort to understand the contribution of nutrient loading to the overgrazing phenomenon including the elevated levels (x32) of generalist urchins in a Caribbean seagrass bed, a detailed isotopic ($\delta^{13}C$, $\delta^{15}N$) assessment of food web structures was conducted both in a nutrient enriched and a control site. The general pattern within the nutrient enriched site showed a significant shift in $\delta^{13}C$ of primary consumers to lighter sources of carbon (i.e. epiphytes, phytoplankton) and increased $\delta^{15}N$ for resources and primary consumers when compared to the control site. The loss of the traditional autochthonous seagrass detritus pool, in the wake of high densities of urchins and low overall consumer diversity, appears to have been partially replaced by opportunistic "alternatives" that benefit directly from elevated input of anthropogenic, allochthonous nutrients. This includes significant increased production of thick filamentous epiphytes and phytoplankton which likely enters the benthic food web as detrital particles. The availability of such alternative resources to generalist urchins, in conjunction with other flexible life history traits, could potentially allow for the existence of a new state where high densities of urchins continue to suppress "traditional" benthic macrophyte production through grazing and the recruitment of competitors and predators through intra-guild predation.

Introduction

Nutrient enrichment of riverine, estuarine and littoral marine systems has become a significant factor in the alteration of benthic food web structure and has been directly linked to dramatic increases in coastal urbanization, associated production of organic sewage and/or the increased use of agricultural fertilizers within adjacent watersheds (McClelland and Valiela 1998b, Cloern 2001, deBruyn and Rasmussen 2002, Grall and Chauvaud 2002). Such elevations in nutrients (eutrophication) often result in increased primary production of nutrient-limited, opportunistic autotrophs (e.g. epiphytes, phytoplankton) and associated detritus at the expense of light-limited macrophytes (e.g. seagrasses) as many aspects of water quality become degraded and consumer diversity is eroded (Pearson and Rosenberg 1978, Duarte 1995, Short and Wyllie-Echeverria 1996, Nixon and Buckley 2002).

The importance of including allochthonous inputs (i.e. spatial subsidies) into food web dynamics has been highlighted in a number of recent papers (Polis and Strong 1996, Polis et al. 1997, Huxel and McCann 1998, Jefferies 2000, Iken et al. 2001, Moore et al. 2004, Polis et al. 2004). Such allochthonous resources (e.g. nutrients, carbon) have been shown to greatly increase the number of consumers which are able to occupy a given habitat while such increased consumer density may at the same time depress autochthonous resource pools. However, due to the allochthonous nature (i.e. donor-controlled) of these resources, including those derived directly or indirectly through anthropogenic nutrient loading, such systems can remain stable even as complexity is lost and a single, large flow of energy dominates the system (Huxel and McCann 1998). Such a fundamental shift in nutrient and carbon availability is expected to affect growth and feeding dynamics, relative abundance of consumer functional groups as well as the overall diversity and carrying capacity of the community (McClelland and Valiela 1998a, Deegan et al. 2002, Huxel et al. 2004).

In many macrophyte-dominated marine systems sea urchins have increased their populations to become the dominant consumers which has in turn reduced macrophyte cover and community biodiversity with extreme overgrazing events leading to the formation of barrens (McGlathery 1995, Sala et al. 1998, Rose et al. 1999, Steneck et al. 2002). Although such dramatic community changes have been associated with predator and competitor release of sea urchins, the contribution and potential significance of nutrient loading should not be ignored (Sala et al. 1998, Steneck et al. 2002). Increased nutrient availability (bottom-up) and grazing pressure (top-down) may in fact work synergistically to influence community changes in these systems (Lapointe 1997, Menge 2000, Nystrom et al. 2000, Jackson et al. 2001).

Naturally occurring heavy isotopes of carbon and nitrogen allow food sources ($\delta^{13}C$) and trophic position ($\delta^{15}N$) of organisms to be determined with reasonable confidence (Fry 1982, Peterson and Fry 1987, Stoner and Waite 1991, Hobson and Welch 1992). Consumers acquire stable isotope signatures through their diet (uptake of nutrients for producers) with a negligible enrichment in the $\delta^{13}C$ (France and Peters 1997) and an approximately 3.4 ‰ enrichment in $\delta^{15}N$ pools. The high trophic position of humans, expressed through sewage-derived nutrients, is reflected in the receiving bodies of water and resident organisms at all trophic levels. The use of $\delta^{15}N$ therefore allows the detection and relative quantification of sewage-derived nutrient enrichment in aquatic food webs (Cabana and Rasmussen 1996, McClelland et al. 1997, Udy et al. 1999). Stable isotopes may also be used to estimate the more detailed contribution of various food sources to the diet of consumers (Hobson 1999, Phillips 2001, Phillips and Gregg 2003).

In this study we examine the influence of nutrient loading on the structure of seagrass food webs with particular attention to the loss in "traditional" detrital resources (i.e. seagrass detritus) and the substantially elevated densities of generalist, pollution-tolerant consumers (i.e. *Lytechinus variegates*). It is hypothesized that the increased availability of nutrients, arriving from the adjacent watershed, has allowed "new" allochthonous and/or "expanded" autochthonous resource pools (i.e. opportunistic autotrophs) to form that are subsequently utilized by the pollution-tolerant generalist urchins to expand and maintain their populations. In an effort to substantiate this hypothesis and identify the specific source(s) of the "new" and/or "expanded" resources, stable isotopes were used to compare this system to a "pristine" (control) seagrass community. We constructed food webs using autotrophs and associated detritus as well as primary and secondary consumers and looked for general community, functional group, and species specific shifts of $\delta^{13}C$ and $\delta\ ^{15}N$ in tissues. We also analysed the composition of specific consumer diets (representatives of the various functional groups) using diet field polygons and mixing model software that incorporated up to six food sources. The "new" and "expanded" resources, made possible through external (allochthonous) nutrient loading, are thought to include increased production of phytoplankton which enters the benthic food web as phytoplankton detritus (allochthonous), thick filamentous forms of epiphytes (autochthonous) and more edible (i.e. lower C:N ratios) *Thalassia* seagrass (autochthonous). The understanding and identification of shifts in resource availability in nearshore systems is essential in light of significant efforts for rehabilitation of such systems after long-term impacts from nutrient loading, sedimentation and other anthropogenic derived perturbations such as overfishing.

Material & Methods

Study Sites

All transect surveys and collections of material for isotopic analyses were conducted in June 2001 and February to June 2002 in the South-western Dominican Republic at a depth of 5-7 metres approximately two hundred metres from shore. Site one was located on the remote western side of the Pedernales peninsula at Baja de las Aguiles within the marine boundaries of Parque Nacional Jaragua providing a site with relatively limited anthropogenic influence (e.g. low nutrient enrichment) (Fig.1). Site two was located on the eastern side of the Pedernales peninsula within the inner harbour of the provincial capital, Barahona (human pop. approx. 100 000), where extensive influence of urbanization including long-term nutrient enrichment had occurred (Fig. 1).

Ambient benthic community conditions

The ambient conditions at the two study sites were assessed along 60 x 3 metre transects (n=6 per site) using measures of benthic producers (*Thalassia testudinum, Syringodium filiforme* and seagrass epiphytes) and detritus biomass as well as mega-invertebrate consumer densities and diversity (Shannon-Weiner Index). The benthic resources were measured within 0.25 x 0.25 m quadrats placed at 20, 40 and 60 m along the transect. All aboveground detritus (up to 1 cm^2) and living seagrass was removed and placed separately into whirlpacks. *Thalassia* leaves were then gently scraped to remove epiphytic biomass which was put into 7 ml plastic vials. All materials were then dried separately for approximately 24 hours at 80° C then weighed on an electronic balance to the nearest 0.01 gram. Epiphytes were acid-washed (24 hrs in 10% HCl) to remove proportionately significant amounts of carbonate, that would otherwise significantly effect measurements of biomass, and dried again for 24 hrs at 80° C. Biomass of all resources were later expressed as grams of dry weight per square metre (gDW/m^2).

Mega-invertebrate consumer densities and subsequent diversity indices were assessed within the 180 m^2 transects by carefully searching through macrophytes, identifying all large animals encountered on and partially in the sediment (16 taxa, see Appendix 1 for 10 principal species used in isotopic analysis) and expressed as the number of individuals per hectare. The Shannon-Weiner method, which combines presence/absence and proportional abundance of a species, was used to calculate an index of mega-invertebrate community diversity. Consumer functional groups were established as follows: a) epiphyte/detritus meiofauna specialists (*Strombus gigas, S. costatus, S. raninus, S. pugilus*); b) generalists (*Lytechinus variegates, Tripneustes ventricosus, Diadema antillarium,*); c) sub-surface deposit feeders: *Meoma venrticosa*, sand dollars; d) surface deposit feeders (*Oreaster reticulates,* sea cucumbers) and e) suspension feeders (*Pinna carnea, Cassiopea spp.*). Invertebrate predators/scavengers (*Murex spp, Pleuroploca gigantean, Cassis sp.*) were also encountered and included in the calculation of diversity although their densities were very low.

Two-sample t-tests were conducted, using SYSTAT version 10.2 (SYSTAT Software Inc. 2002), to examine differences between ambient conditions at the two sites. All analyses were carry out using log (n+0.03) gDW/m^2 and log (n+10) indiv./ha transformed values for resources and primary consumers respectively. These transformations reflect appropriate minimum detection limits over mean sample values (0.03 g and 10 indiv.) and address potential non-normal distributions. Untransformed data (Shannon-Weiner index) was used to examine differences in diversity.

Stable Isotope Analysis

Samples of phytoplankton and associated particulate organic material (POM), sediment organic material (SOM) including various forms of particulate detritus, living seagrasses (*Thalassia testudinum, Syringodium filiforme*), seagrass detritus (largely *Thalassia*), seagrass epiphytes, mega-invertebrates (molluscs, echinoderms), fish as well as some stomach contents were collected. Water samples (≈ 2 L) for POM were collected at one metre below the surface and vacuum pumped onto pre-combusted (550°C for 24 hrs.) Whatman GF/F filters (0.45 μm pore size). Surface sediments (≈ 400 g) were collected and placed into a beaker, stirred, with the resulting suspension decanted off and vacuum pumped onto pre-combusted Whatman GF/F filters. Muscle tissue was sampled from mollusc and fish species. Test and test linings were sampled from echinoids (urchins, heart urchins) and arms tips were sampled from asteroids (starfish). All GF/F filters and tissue samples were dried for 24hrs at 80° C for transport back to the McGill University. All samples, with the exception of GF/F filters, were later acid-washed (24 hrs in 10% HCl) to remove carbonates (which could interfere with δ^{13}C signals), rinsed with distilled water, dried again for 24 hrs at 80° C, ground to a fine powder and packed into 4 mm x 6 mm tin capsules. The stable isotope analysis for these materials was performed at the G.G. Hatch laboratories, Department of Earth Sciences, University of Ottawa. Stable isotope ratios are expressed in delta units (δ) defined as parts per thousand (°/₀₀) deviations from standard materials, Pee Dee belemnite limestone for δ^{13}C and atmospheric nitrogen for δ^{15}N. Replicate samples (N=24) showed good technical precision for $\delta\ ^{13}$C (±0.24 °/₀₀) and $\delta\ ^{15}$N signals (±0.19 °/₀₀). GF/F filters were acid-washed with 10% HCl, then rinsed with distilled water by vacuum pump, then dried for 24 hrs. The analyses for GF/F bound material (POM, SOM) was preformed at Centre GEOTOP-UQAM-McGill, Université du Québec à Montréal. Precision on all GEOTOP results were approximately ±0.1 °/₀₀ and ±0.5 °/₀₀ for $\delta\ ^{13}$C and $\delta\ ^{15}$N respectively. Again, two-sample t-tests were conducted, using SYSTAT version 10.2, to examine differences between stable isotope values at the two sites.

Mixing models

The limitations of using geometric procedures to determine dietary contributions of three or more food sources using $\delta^{13}C$ and $\delta^{15}N$ (Phillips 2001, Schindler and Lubetkin 2004) and the broad range of consumers and potential food sources involved in this study (up to 6) called for the use of the software package IsoSource (Phillips and Gregg 2003) in determining feasible bounds for the contribution of food sources to consumer tissues. Further restrictions on potential dietary components were imposed based on the general known ecology of the consumers (i.e. functional group and associated feeding ecology) and the ambient conditions of the model systems examined (e.g. no *Syringodium* present at site 2). Mixing polygons were first established by considering all dietary components at each site based on corrected (fractionation of food by consumers during digestion and assimilation) $\delta^{15}N$ at each site due to site specific C:N ratio of diets (Adams and Sterner 2000). Again, we assumed no significant fractionation of carbon (France and Peters 1997). Representative consumers from functional groups, those with the most comprehensive data, were then plotted in relation to the dietary polygon. The actual distribution of feasible contributions to a consumers diet was determined within the IsoSource program (version 1.1) by inputting consumer stable isotope values and $\delta^{13}C$ and corrected $\delta^{15}N$ values for resources. The source increment and mass balance tolerance boundaries used for all calculations were 1% and ±0.25 $^{o}/_{oo}$ respectively and are considered reasonable levels (Phillips and Gregg 2003). A limited number of stomach contents were also processed in this manner. Descriptive statistics for mixed diet analsyses: mean; standard deviation and 1 – 99 percentile ranges, were reported from the IsoSource program.

Results

Ambient benthic community conditions

Biomass estimates (gDW/m^2) for benthic resources at the two sites indicated significantly reduced levels of seagrass detritus and living *Syringodium* and significantly elevated levels of seagrass epiphytes at the impacted site 2, while levels of *Thalassia* were not different (Fig. 2a). Abundance of primary mega-invertebrate consumer functional groups at the nutrient enriched site declined significantly for specialists and sub-surface deposit feeders with neither surface deposit feeders nor suspension feeders changing (Fig. 2b). The abundance of generalists, almost exclusively the echinoid *Lytechinus variegatus*, increased over two orders of magnitude and represented 98.5% of primary consumer abundance at site two (Fig. 2b). The Shannon-Weiner diversity index declined significantly ($p = 0.0016$) from 1.48 (±0.17, SD) at site one to 0.23 (±0.35) at site two.

Food Web Configuration and Stable Isotope Shifts

All species used in the formulation of the two foodwebs are considered ubiquitous across the Caribbean region and occurred at both sites, with the exceptions of the seagrass *Syringodium filiforme* and the molluscan predator *Cassis spp.* (Appendix 1). In general, there was a shift of $\delta^{13}C$ to lighter sources and an increase of about 3 delta units in the $\delta^{15}N$ across the entire food web examined at site two (Fig. 3). The $\delta^{13}C$ shift was most pronounced and significant ($p < 0.05$) for some non-generalist primary consumers (*S. gigas, Meoma ventricosa, Pinna carnea*) as well as for SOM (Fig. 3, Appendix 1). Significant ($p < 0.02$) increases in $\delta^{15}N$ were noted for all traditional benthic resources (*Thalassia* and associated epiphytes and detritus) as well as all primary consumers (Appendix 1). Amongst stable isotopes of stomach contents only the $\delta^{13}C$ of the sub-surface deposit feeding *Meoma ventricosa* displayed a marginally significant ($p = 0.056$) lighter signal at site two (Table 1).

Mixing Models

Mixing polygons were established for each site by plotting the $\delta^{13}C$ (no fractionation assumed) and adjusted $\delta^{15}N$ values of all potential dietary components for representatives of consumer functional groups (specialists, *S. gigas*; deposit feeders, *M. ventricosa*; suspension feeders, *P. carnea*; generalists, *L. variegatus*) (Fig. 4). The adjusted $\delta^{15}N$, due to fractionation, was based on the mean (± SD) fractionation value of all feasible diet components (based on known ecology and available resources) for all representative consumers (site 1: 1.93‰ ± 0.36, site 2:

3.31°/₀₀ ± 0.28) (Fig. 4). The known ecology of specialists excluded POM and living seagrasses from their diet with deposit and suspension feeding diets having living seagrasses excluded (Chesher 1969, Stoner and Waite 1991, Kennedy et al. 2001). This then reduced the overall bounds of the diet field for these particular functional groups (see caption, Fig. 4). Unfortunately, the intermediate position of some consumers with respect to feasible diet components, most notably *L. variegates* (Fig. 4a), within the diet field resulted in imprecise, wide-ranging solutions.

The results from the mixing model (IsoSource, Appendix 2) agree fairly well with the known feeding ecology and qualitative observations using diet field polygons (Fig. 4). Mixing model results concentrated on diet components that showed the most constrained solutions with less emphasis on imprecise ones. Specialist, *S. gigas*, relies on epiphytes (50%) and SOM (42%) with some minor but increasing (+7%) use of seagrass detritus at site 2 (Fig. 5). The deposit feeding *M. ventricosa* uses seagrass detritus heavily (> 71%) with a more substantial contribution of SOM (+17%) at site 2 (Fig. 5). The suspension feeding bivalve *P. carnea* does utilize POM (24%) at site one but with a greater contribution of detritus (40%), likely in re-suspended form. POM becomes a minor component (< 8%) at site 2 as SOM (18%) seemingly replaces it, with detritus (41%) remaining of major importance. Finally, the generalist echinoid *Lytechinus* shows a well mixed diet, with detritus (> 21%) and epiphytes (> 22%) appearing to be important at both sites (Fig. 5), although solutions are quite imprecise. Also, living *Thalassia* (31%) may become important at site 2 (+13%) (Fig. 5). Limited analysis of stomach contents verify the potential importance of living *Thalassia* (53%) for *Lytechinus* at site 2 as well as the contributions of POM (34%) and SOM (59%) to *Pinna* at site 1 (Table 2). Feasible solutions using the IsoSource software were not found for stomach samples of *M. ventricosa* or *S. gigas*.

Finally, given the suspected mixed nature of SOM at both sites IsoSource was used to evaluate its constituent components. Feasible mixtures of POM, epiphytes and seagrass detritus were generated using only $\delta^{13}C$. Substantial changes in the contribution of POM (7% to 44%) and seagrass detritus (57% to 24%) to the SOM mixture were found between site 1 and site 2 with only minor changes in epiphytes (36% to 32%) (Table 2).

Discussion

The very high abundances of generalist urchins (i.e. *Lytechinus variegatus*) observed within a Caribbean seagrass food web impacted by significant nutrient enrichment (elevated $\delta^{15}N$ across the site 2 food web, (Cabana and Rasmussen 1996)) spawned the question as to how such increased numbers could be supported in light of the accompanying simplified community structure and absence of some traditional resources including substantial decreases in seagrass detritus. In this study we used stable isotopes of carbon and nitrogen, within both the nutrient enriched and largely pristine control site, in combination with more conventional survey work, to reveal the existence and use of alternative resources by generalist primary consumers (Fig. 5). These alternative resources, both autochthonous and allochthonous forms, are available to the surviving benthic consumer community indirectly as a consequence of elevated levels of nutrients utilized by opportunistic autotrophs including phytoplankton, epiphytes, stress tolerant/competitive *Thalassia* and associated detritus from all sources.

Narrowing traditional food base and loss of consumer diversity

As we examine the traditional resource base within Caribbean seagrass communities, noting that the bulk of organic transfer in these systems to higher trophic levels is traditionally via the detrital pathway (Vadas et al. 1982, Stoner et al. 1995, Pomeroy 2001, Vizzini et al. 2002), it is quite striking to observe the very low levels of seagrass derived-detritus at the nutrient-enriched site. This may cause significant changes in trophic structure and community dynamics involved in the physical and chemical breakdown of detritus leading to the observed losses in diversity (Moore et al. 2004). In particular we observed a significant decline amongst specialists and sub-surface deposit feeders that may be more sensitive to the loss of traditional detrital resources. The complete absence of the seagrass *Syringodium filiforme* at the enriched site, is likely related to declines in water quality (i.e. low light due to sediment accretion), competition with *Thalassia* and intense herbivory, *Syringodium* being more edible, by the elevated densities of generalist consumers (i.e. *Lytechinus variegatus*) (Williams 1987, 1990, Cebrian 1998).

Alternate resources support generalist consumers

The narrowing of the "traditional" resource base is in stark contrast to the significant increase in primary consumer abundance (32 times overall, 98.5% *L. variegatus*) and the amount of production that would be required to sustain such high populations. A logical hypothesis would be to consider the availability of "new" or "expanded" resource pools that may be utilized by the abundance of largely generalist consumers.

To begin, there appears to be a significant increase in seagrass epiphytes at the impacted site. This complex of autotrophs should benefit from increased nutrient availability and have previously been identified as contributing significantly to benthic production within seagrass food webs (Kitting et al. 1984, Moncreiff and Sullivan 2001). The species composition of the epiphytic community may change from the typical calcareous red algae found in oligotrophic habitats to thick filamentous species, which we observed, at eutrophic sites (McGlathery 1995). Alternative resources may also include the increased production and edibility of *Thalassia* due to higher nitrogen (i.e. lower C:N ratios) content (McGlathery 1995). The standing biomass values may remain unchanged, as in this study, with increased production being consumed and not evident as either living or seagrass detrital biomass. The increased contribution of living *Thalassia* to the diet of *Lytechinus variegates* at site 2, from approximately 19% to 31%, may corroborate such a hypothesis although the diffuse distribution of dietary components for this consumer demands caution. Also, the significant underutilization of seagrass detritus and unaffected nature of living *Thalassia* within enclosure experiments with *L. variegatus* at the nutrient enriched site casts further doubt on the use of such resources (Tewfik et al., submitted)

Perhaps the most potentially important "new" resource available to urchins may be linked to the most well known consequence of eutrophication – the elevation in phytoplanktonic production (Duarte 1995, Cloern 2001, Nixon and

Buckley 2002). The bulk of this increased production may not be directly consumed as living phytoplankton but may likely enter the benthic food web as an allochthonous subsidy of detrital particulates (i.e. phytoplankton particulate detritus) falling from the pelagic zone which has been shown to support other communities (Iken et al. 2001, Bouillion et al. 2002, Bouillon et al. 2002). Our study shows evidence of such a subsidy with the significant shift in sediment organic material (SOM) $\delta^{13}C$ from -11.9 (site 1) to -20.5 (site 2) in light of a POM signature of approximately -31.0 at both sites and shifts in non-generalist consumer (i.e. *S. gigas*, *Meoma*) $\delta^{13}C$ to significantly lighter values. The large increase of SOM in the composition of some consumer diets (*Meoma*, +18%; *Pinna*, +14%) at the enriched site also supports the hypothesis of a significant phytoplankton detritus based allochthonous subsidy to the benthic community. The substantial shift in the contribution of POM to the SOM mixture, 7% to 44%, and loss of seagrass detritus in SOM, 57% to 24%, from site 1 to site 2 further substantiates the addition of allochthonous (i.e. phytoplankton) dertitus and loss of autochthonous (i.e. seagrass) detritus to the SOM resource pool at the nutrient enriched site. Finally, the morphological plasticity of urchins (e.g. modification of spines) has been shown to facilitate the use of particulate (e.g. phytoplankton detritus) and dissolved forms of organic material (Lawrence 1975, Delmas and Regis 1984, Regis 1986, Beddingfield and McClintock 1998) which may be expected to be elevated at nutrient enriched sites (McClelland and Valiela 1998b, Nixon and Buckley 2002).

Conclusions

Macrophyte-dominated communities in temperate and tropical latitudes represent important benthic ecosystems where the effects of overfishing and nutrient loading have caused significant changes in food web structure and loss of ecosystem services (McClelland and Valiela 1998a, Jackson 2001, Deegan et al. 2002) Although overgrazing of macrophyte dominated systems (e.g. California, Mediterranean, Eastern Canada) has largely been attributed to predator and competition release of urchins due to overfishing the contribution and significance of nutrient loading has been suggested (Sala et al. 1998, Steneck et al. 2002). The loss of sensitive species under chronic pollution stress may coincide with the increase in other stress-tolerant forms that have the capacity to endure these changes, in conjunction with the appearance of "new" and "expanded" resource pools (i.e. nutrients and carbon), and remain for long periods of time.

This may be of particular relevance in the Caribbean where destructive overgrazing within seagrasses has been documented (Camp et al. 1973, Macia and Lirman 1999, Rose et al. 1999), significant increases in urbanization and associated nutrient loading within protected coastal lagoons is under way (McGlathery 1995) and the levels of urban sewage treatment are largely inadequate (Siung-Chang 1997). Such a scenario may be a near ideal combination of parameters to allow increases in the number of generalist urchins, indirectly through increased availability of opportunistic autotophs, that may erode diversity as they strongly suppress autochthonous resources and competitive consumers through grazing and intra-guild predation (Polis and Strong 1996, Rose et al. 1999).

The extremely flexible generalist diet of sea urchins as well as other strategies including the reduction of metabolism, re-absorption of body tissues, and recruitment from distant populations, may allow urchins to maintain densities even after overgrazing (Ebert 1967, Duggins 1980, Tegner and Levin 1982, Miller 1985). Our study strongly suggests that the input of anthropogenic nutrients (eutrophication) to opportunistic autotrophs forms important new or expanded resources, including phytoplankton detritus, allowing the existence and potential long-term persistence of significantly elevated numbers of generalist urchins. This may be a fundamental issue in the identification of changes in community structure within nearshore marine systems and the realization of goals of rehabilitating such areas after decades of nutrient loading and overfishing stress.

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Literature Cited

Adams, T., and R. Sterner. 2000. The effect of dietary nitrogen content on trophic level ^{15}N enrichment. Limnology and Oceanography 45:601-607.

Beddingfield, S. D., and J. B. McClintock. 1998. Differential survivorship, reproduction, growth and nutrient allocation in the regular echinoid *Lytechinus variegatus* (Lamarck) fed natural diets. Journal of Experimental Marine Biology and Ecology 226:195-215.

Bouillion, S., A. Raman, P. Dauby, and F. Dehairs. 2002. Carbon and nitrogen stable isotope ratios of subtidal benthic invertebrates in an esturine mangrove ecosystem (Andhra Pradesh, India). Estuarine, Coastal and Shelf Science 54:901-913.

Bouillon, S., N. Koedam, A. Raman, and F. Dehairs. 2002. Primary producers sustaining macro-invertebrate communities in intertidal mangrove forests. Oecologia 130:441-448.

Cabana, G., and J. B. Rasmussen. 1996. Comparison of aquatic food chains using nitrogen isotopes. Proceedings of the National Academy of Science of the United States of America 93:10844-10847.

Camp, D. K., S. P. Cobb, and J. F. van Breddveld. 1973. Overgrazing of grasses by a regular urchin, *Lytechinus variegatus*. Bioscience 23:37-38.

Cebrian, J. D., C.M. 1998. Patterns in leaf herbivory on seagrass. Aquatic Botany 60:67-82.

Chesher, R. H. 1969. Contributions to the biology of Meoma ventricosa. Bulletin of Marine Science 19:72-110.

Cloern, J. E. 2001. Our evolving conceptual model of the coastal eutrophication problem. Marine Ecology Progress Series 210:223-253.

deBruyn, A., and J. Rasmussen. 2002. Quantifying assimilation of sewage-derived organic matter by riverine benthos. Ecological Applications 12:511-520.

Deegan, L. A., A. Wright, and S. G. e. a. Ayvanazian. 2002. Nitrogen loading alters seagrass ecosystem structure and support of higher trophic levels. Aquatic Conservation: Marine and Freshwater Ecosystems 12:193-212.

Delmas, P., and M. Regis. 1984. Influence d'une pollution complexe a dominante domestique sur les populations de l'echinoide comestible *Paracentrotus lividis* (Lamark). Vie marine 6:63-72.

Duarte, C. M. 1995. Submerged aquatic vegetation in relation to different nutrient regimes. Ophelia 41:87-112.

Duggins, D. O. 1980. Kelp beds and sea otters: an experimental approach. Ecology 61:447-453.

Ebert, T. A. 1967. Negative growth and longevity in purple sea urchin *Strongylocentrotus purpuratus* (Stimpson). Science 157:557-558.

France, R., and R. Peters. 1997. Ecosystem differences in the trophic enrichment of ^{13}C in aquatic food webs. Canadian Journal of Fisheries and Aquatic Sciences 54:1255-1258.

Fry, B. L., R; Northam, M; Parker, P. 1982. A 13C/12C comparison of food webs in Caribbean seagrass meadows and coral reefs. Aquatic Botany 14:389-398.

Grall, J., and L. Chauvaud. 2002. Marine eutrophication and benthos: the need for new approaches and concepts. Global Change Biology 8:813-830.

Hobson, K. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120:314-326.

Hobson, K. A., and H. E. Welch. 1992. Determination of trophic relationships within high Arctic marine food webs using 13C and 15N analysis. Marine Ecology Progress Series 84:9-18.

Huxel, G., G. Polis, and R. Holt. 2004. At the frontier of the integration of food web ecology and landscape ecology. Pages 434-451 *in* G. Polis, M. Power, and G. Huxel, editors. Food webs at the landscape level. The University of Chicago Press, Chicago.

Huxel, G. R., and K. S. McCann. 1998. Food web stability: The influence of trophic flows across habitats. American Naturalist 152:460-469.

Iken, K., T. Brey, U. Wand, J. Voigt, and P. Junghans. 2001. Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. Progress in Oceanography 50:383-405.

Jackson, J. B. C. 2001. What was natural in the coastal oceans? Proceedings of the National Academy of Science of the United States of America 98:5411-5418.

Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. B.J., R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629-638.

Jefferies, R. 2000. Allochthonous inputs: integrating population changes and food-web dynamics. Trends in Ecology and Evolution 15:19-22.

Kennedy, H., C. A. Richardson, C. M. Duarte, and D. P. Kenedy. 2001. Diet and association of *Pontonia pinnphylax* occuring in *Pinna nobilis:* insights from stable isotope analysis. Journal of the Marine Biological Association of the United Kingdom 81:177-178.

Kitting, C., B. Fry, and M. Morgan. 1984. Detection of inconspicuous epiphytic algae supporting food webs in seagrass meadows. Oecologia 62:145-149.

Lapointe, B. E. 1997. Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. Limnology and Oceanography 42:1119-1131.

Lawrence, J. 1975. On the relationship between marine plants and sea urchins. Oceanography and Marine Biology: an Annual Review 13:213-286.

Macia, S., and D. Lirman. 1999. Destruction of Florida Bay seagrasses by a grazing front of sea urchins. Bulletin of Marine Science 65:593-601.

McClelland, J., and I. Valiela. 1998a. Changes in food web structure under the influence of increased anthropogenic nitrogen inputs to estuaries. Marine Ecology Progress Series 168:259-271.

McClelland, J. W., and I. Valiela. 1998b. Linking nitrogen in esturine producers to land-deived sources. Limnology and Oceanography 43:577-585.

McClelland, J. W., I. Valiela, and R. H. Michener. 1997. Nitrogen-stable isotope signatures in esturine food webs: A record of increasing urbanization in coastal watersheds. Limnology and Oceanography 42:930-937.

McGlathery, K. J. 1995. Nutrient and grazing influences on a subtropical seagrass community. Marine Ecology Progress Series 122:239-252.

Menge, B. A. 2000. Top-down and bottom-up community regulation in marine rocky intertidal habitats. Journal of Experimental Marine Biology and Ecology 250:257-289.

Miller, R. J. 1985. Seaweeds, sea urchins, and lobster: A reappraisal. Canadian Journal of Fisheries and Aquatic Sciences 42:2061-2071.

Moncreiff, C. A., and M. J. Sullivan. 2001. Trophic importance of epiphytic algae in subtropical seagrass beds: evidence from multiple stable isotope analysis. Marine Ecology Progress Series 215:93-106.

Moore, J., E. Berlow, D. Coleman, P. de Ruiter, Q. Dong, A. Hastings, N. Collins-Johnson, K. McCann, K. Melville, P. Morin, K. Nadelhoffer, A. Rosmond, D. Post, J. Sabo, K. Scow, M. Vanni, and D. Wall. 2004. Detritus, Trophic Dynamics, and Biodiversity. Ecology Letters 7:584-600.

Nixon, S., and B. Buckley. 2002. "A strikingly rich zone" - Nutrient enrichment and secondary production in coastal marine ecosystems. Estuaries 25:782-796.

Nystrom, M., C. Folke, and F. Moberg. 2000. Coral reef disturbance and resilience in a human-dominated environment. Trends in Ecology and Evolution 15:413-417.

Pearson, T., and R. Rosenberg. 1978. Macrobenthic successions in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology: an Annual Review 16:229-311.

Peterson, B. J., and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18:293-320.

Phillips, D. 2001. Mixing models in analyses of diet using stable isotopes: a critique. Oecologia 127:166-170.

Phillips, D., and J. Gregg. 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia 136:261-269.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology. Annual Review of Ecology and Systematics 28:289-316.

Polis, G. A., M. E. Power, and G. R. Huxel. 2004. Food webs at the landscape level. The University of Chicago Press, Chicago.

Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. American Naturalist 147:813-846.

Pomeroy, L. 2001. Caught in the food web: complexity made simple? Scientia Marina 65:31-40.

Regis, M. 1986. Microstructure adaptive des radioles de *Paracentrotus lividus* (Echinodermata: Echinoidea) en milieu eutrophise par des eaux usees. Marine Biology 90:271-277.

Rose, C. D., W. C. Sharp, W. J. Kenworthy, J. H. Hunt, W. Lyons, G,, E. J. Prager, J. F. Valentine, M. O. Hall, P. E. Whitfield, and J. W. Fourqurean. 1999. Overgrazing of a large seagrass bed by the sea urchin *Lytechinus variegatus* in Outer Florida Bay. Marine Ecology Progress Series 190:211-222.

Sala, E., C. F. Boudouresque, and M. Harmelin-Vivien. 1998. Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. Oikos 82:425-439.

Schindler, D., and S. Lubetkin. 2004. Using sable isotopes to quantify material transport in food webs. Pages 25-42 *in* G. Polis, M. Power, and G. Huxel, editors. Food webs at the landscape level. The University of Chicago Press, Chicago.

Short, F. T., and S. Wyllie-Echeverria. 1996. Natural and human-induced disturbance of seagrasses. Environmental Conservation 23:17-27.

Siung-Chang, A. 1997. A review of marine pollution issues in the Caribbean. Environmental Geochemistry and Health 19:45-55.

Steneck, R. S., M. Graham, B. Bourque, D. Corbett, J. Erlandson, J. Estes, and M. Tegner. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. Environmental Conservation 29:436-459.

Stoner, A. W., M. Ray, and J. M. Waite. 1995. Effects of a large herbivorous gastropod on macrofauna communities in tropcal seagrass meadows. Marine Ecology Progress Series 121:125-137.

Stoner, A. W., and J. M. Waite. 1991. Trophic biology of *Strombus gigas* in nursery habitats: Diets and food sources in seagrass meadows. J Moll. Stud. 57:451-460.

Tegner, M. J., and L. A. Levin. 1982. Do sea urchins and abalones compete in California? Pages 265-271 *in* J. M. Lawrence, editor. International Echinoderms Conference. A.A. Balkema, Rotterdam, Netherlands, Tampa Bayida, Florida.

Udy, J. W., W. C. Dennison, W. J. L. Long, and L. J. McKenzie. 1999. Responses of seagrass to nutrients in the Great Barrier Reef, Australia. Marine Ecology Progress Series 185:257-271.

Vadas, R. L., T. Fenchel, and J. C. Ogden. 1982. Ecological studies of the sea urchin, *Lytechinus variegatus*, and the algal-seagrass communities of the Miskito Cays, Nicaragua. Aquatic Botany 14:109-125.

Vizzini, S., G. Sara, R. H. Michener, and A. Mazzola. 2002. The role and contribution of seagrass *Posidonia oceanica* (L.) Delile organic matter for secondary consumers as revealed by carbon and nitrogen stable isotope analysis. Acta Oecologica 23:277-285.

Williams, S. L. 1987. Competition between the seagrasses *Thalassia testudinum* and *Syringodium filiforme* in a Caribbean lagoon. Marine Ecology Progress Series 35:91-98.

Williams, S. L. 1990. Experimental studies of Caribbean seagrass bed development. Ecological Monographs 60:449-469.

Tables

Table 1: Mean δ^{13}C and $\delta\,^{15}$N (± 1 se) data from stomach contents of primary consumers. n = sample size. * paired t-test for $\delta\,^{13}$C (p = 0.056).

Consumer	Site	δ 13C	δ 15N	n
Strombus gigas	1	-11.7 ± 0.3	1.0 ± 0.3	3
	2	n/a	n/a	
Lytechinus variegatus	1	-10.6 ± 1.0	0.4 ± 0.8	2
	2	-11.3 ± 0.9	3.9 ± 0.5	5
Meoma ventricosa *	1	-13.2 ± 0.1	n/a	2
	2	-14.4 ± 0.0	3.0 ± 0.2	2
Pinna carnea	1	-18.3	0.7	1
	2	n/a	n/a	

Table 2: Mixing model results from consumer stomach contents based on δ^{13}C and corrected δ^{15}N and sediment organic material (SOM). Statistics include mean, standard deviation (SD) and 1 – 99 percentile ranges. Blank cells indicate resources not readily available to that particular consumer. Viable solutions were not available for missing consumers and sites. * based only on δ^{13}C.

Consumer	Site	Statistics	POM	SOM	detritus	*Thalassia*	*Syringodium*	epiphytes
Lytechinus variegatus	1	mean	5.6	15.2	22.6	19.9	16.3	20.4
		SD	3.1	9.6	16.7	14.2	10.6	14.5
		range	0 - 12	0 - 38	0 - 67	0 - 55	0 - 42	0 - 56
	2	mean	4.7	1.2	17.6	52.9		23.6
		SD	3.3	1.2	1.3	16.4		12.5
		range	0 - 11	0 - 4	0 - 50	12 - 84		0 - 46
Pinna carnea	1	mean	33.6	59.4	2.8			4.2
		SD	0.9	3.2	2.4			3.6
		range	32 - 35	53 - 66	0 - 9			0 - 13
SOM *	1	mean	7.2		56.6			36.2
		SD	4.5		16.8			21.2
		range	0 - 15		26 - 85			0 - 73
	2	mean	44.1		24.4			31.5
		SD	4.4		14.4			18.7
		range	36 - 52		0 - 49			0 - 63

Figures

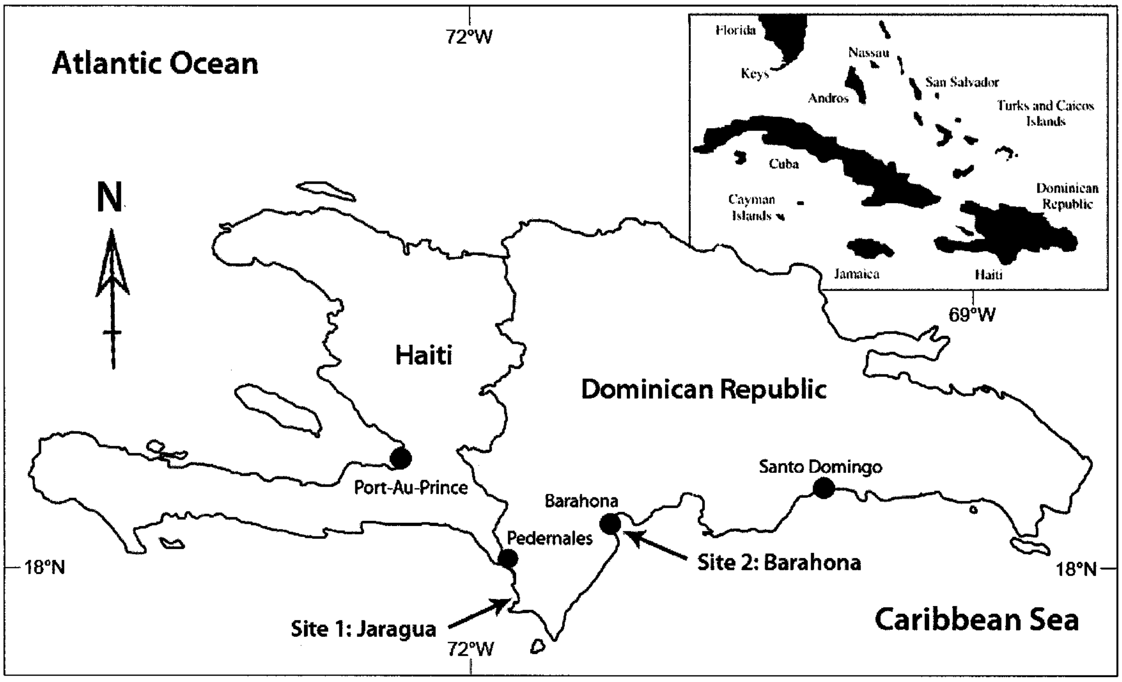

Fig. 1: Map of Hispaniola (Inset: location of Hispaniola in the Central Caribbean) and location of seagrass beds sampled in South-western Dominican Republic. Site 1 (Jaragua National Park): low nutrient enrichment, Site 2 (Barahona, provincial capital): high nutrient enrichment.

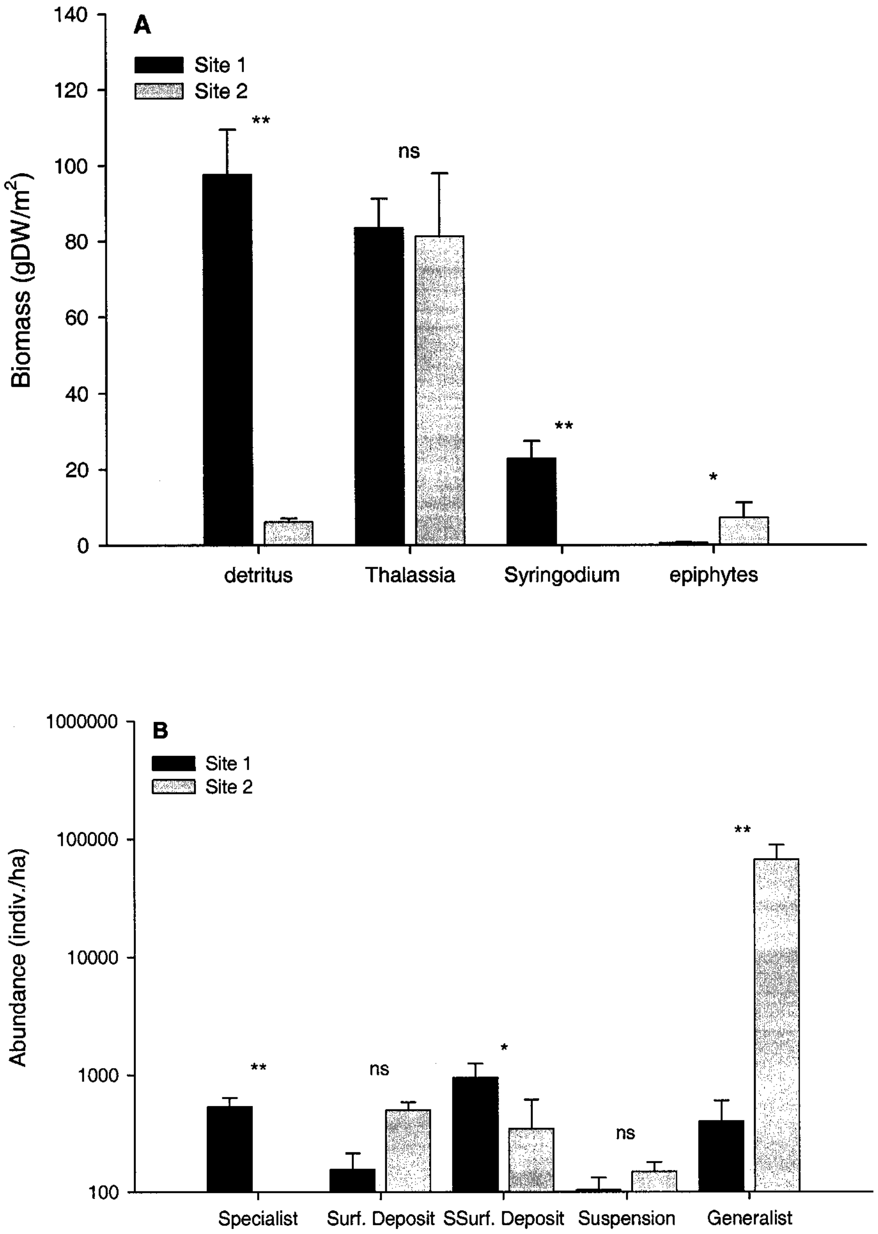

Fig 2: Distribution of mean (± 1 se) values for A) benthic resources (primary producers and detritus, gDW/m^2) and B) mega-invertebrate primary consumer functional groups (Surf. = Surface, SSurf. = Sub-surface) (individuals/ha) at site 1 (low nutrient enrichment) and site 2 (high nutrient enrichment), Southwestern, Dominican Republic. Paired t-test results (site 1 vs. site 2) for benthic resources, log (n+0.03): * $P < 0.05$; ** $P < 0.0005$; ns = not significant. Paired t-test results (site 1 vs. site 2) for consumers, log (n+10): * $P < 0.05$; ** $P < 0.005$; ns = not significant.

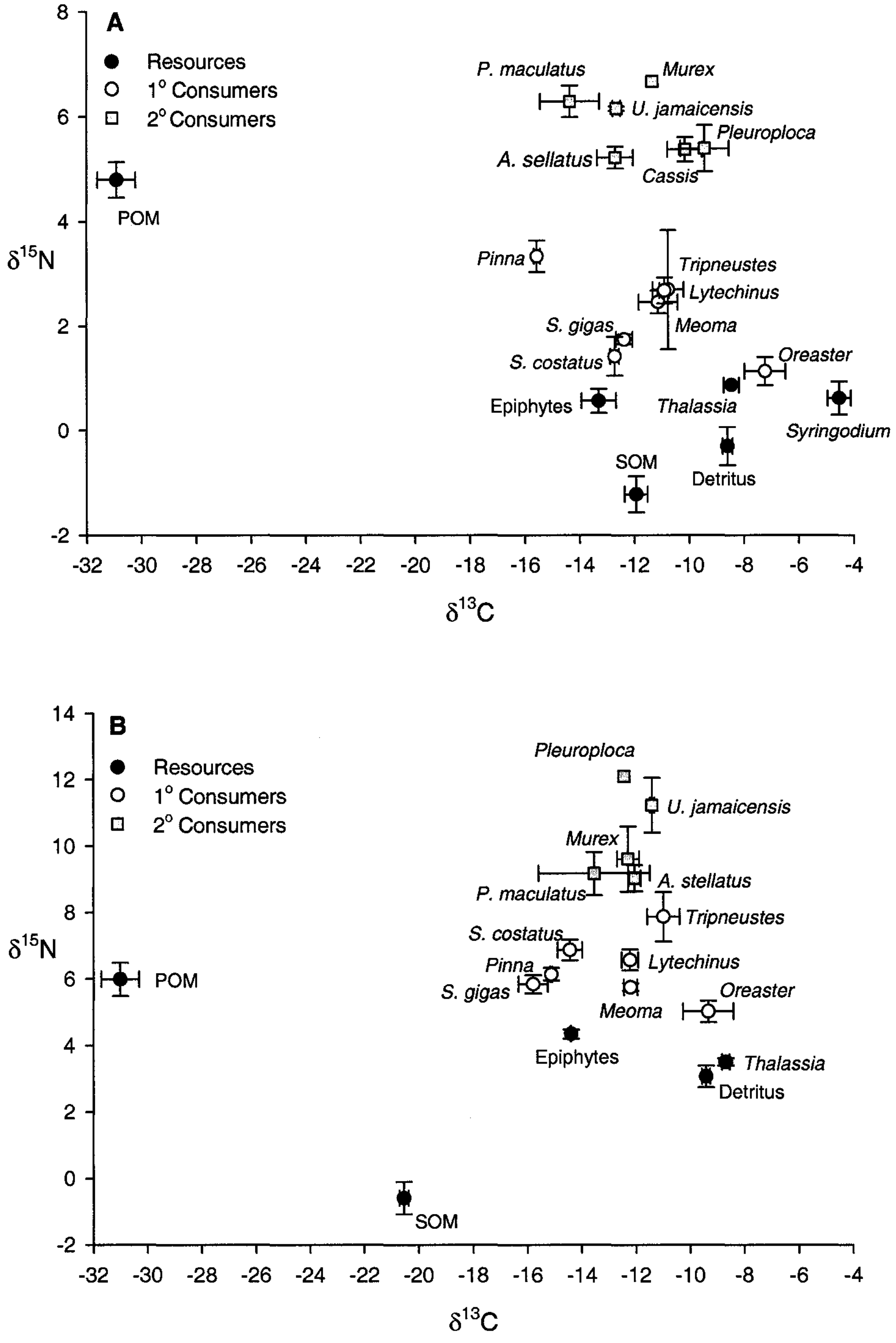

Fig. 3: Mean $\delta^{15}N$ vs. $\delta^{13}C$ (± 1 se) for benthic resources (primary producers and detritus), primary and secondary consumers at A) site 1 (low nutrient enrichment) and B) site 2 (high nutrient enrichment), Dominican Republic. See appendix 1 for details on common names, and sample statistics.

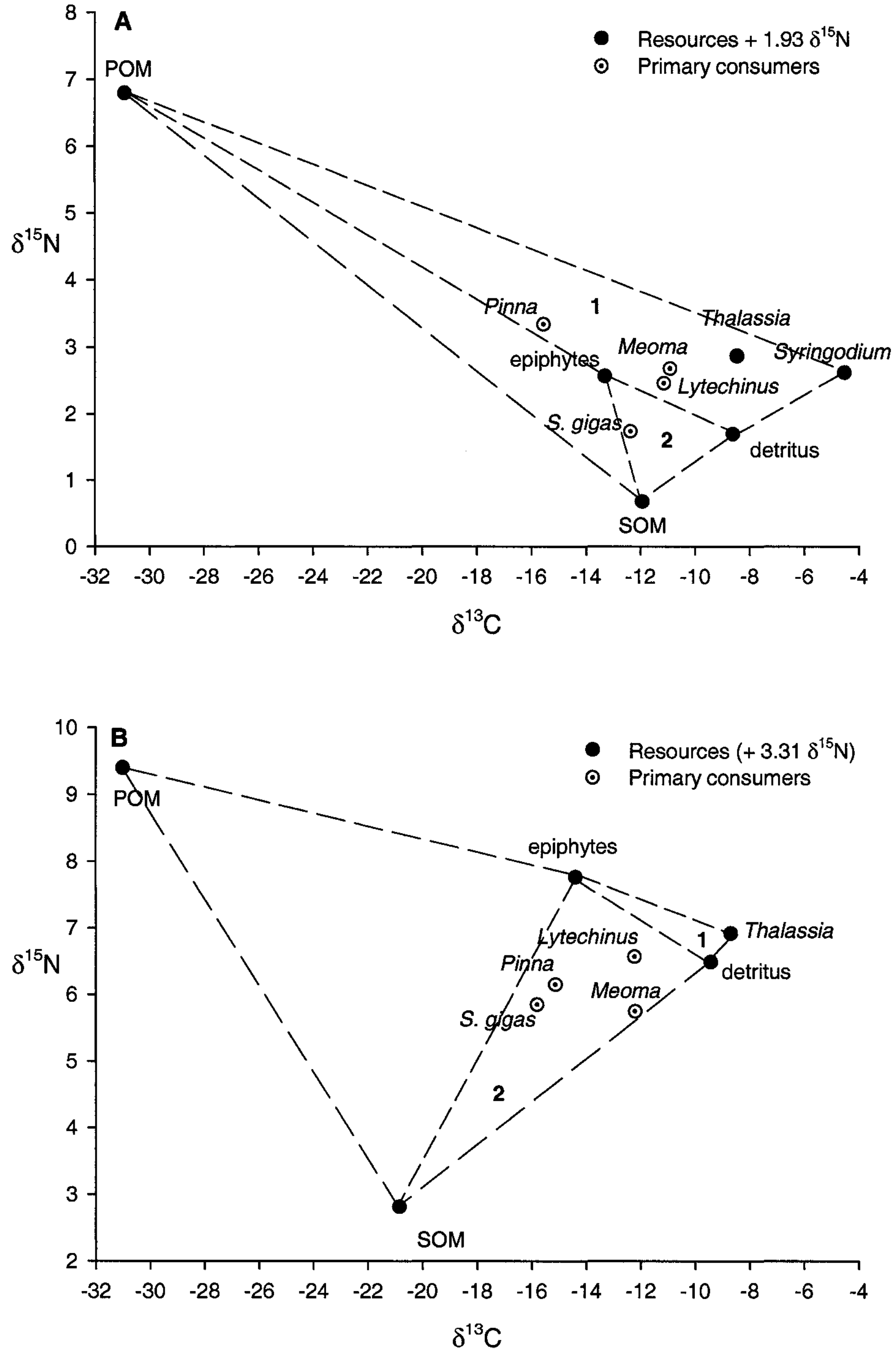

Fig. 4: Mixing polygons for $\delta^{13}C$ and $\delta^{15}N$ signatures of food sources for benthic mega-invertebrate primary consumers at A) site 1 (low nutrient enrichment) and B) site 2 (high nutrient enrichment), Dominican Republic. $\delta^{15}N$ signatures are adjusted by 1.93 and 3.31 delta units for A and B respectively to correct for trophic fractionation of nitrogen which is influenced by different C:N ratios at specific sites. Area **1** included for *Lytechinus variegatus* only and area **2** is total diet field for *Strombus gigas*. Primary consumers represent functional groups: *S. gigas* (specialist); *L. variegatus* (generalist); *Meoma ventricosa* (Deposit feeder); *Pinna carnea* (Suspension feeder).

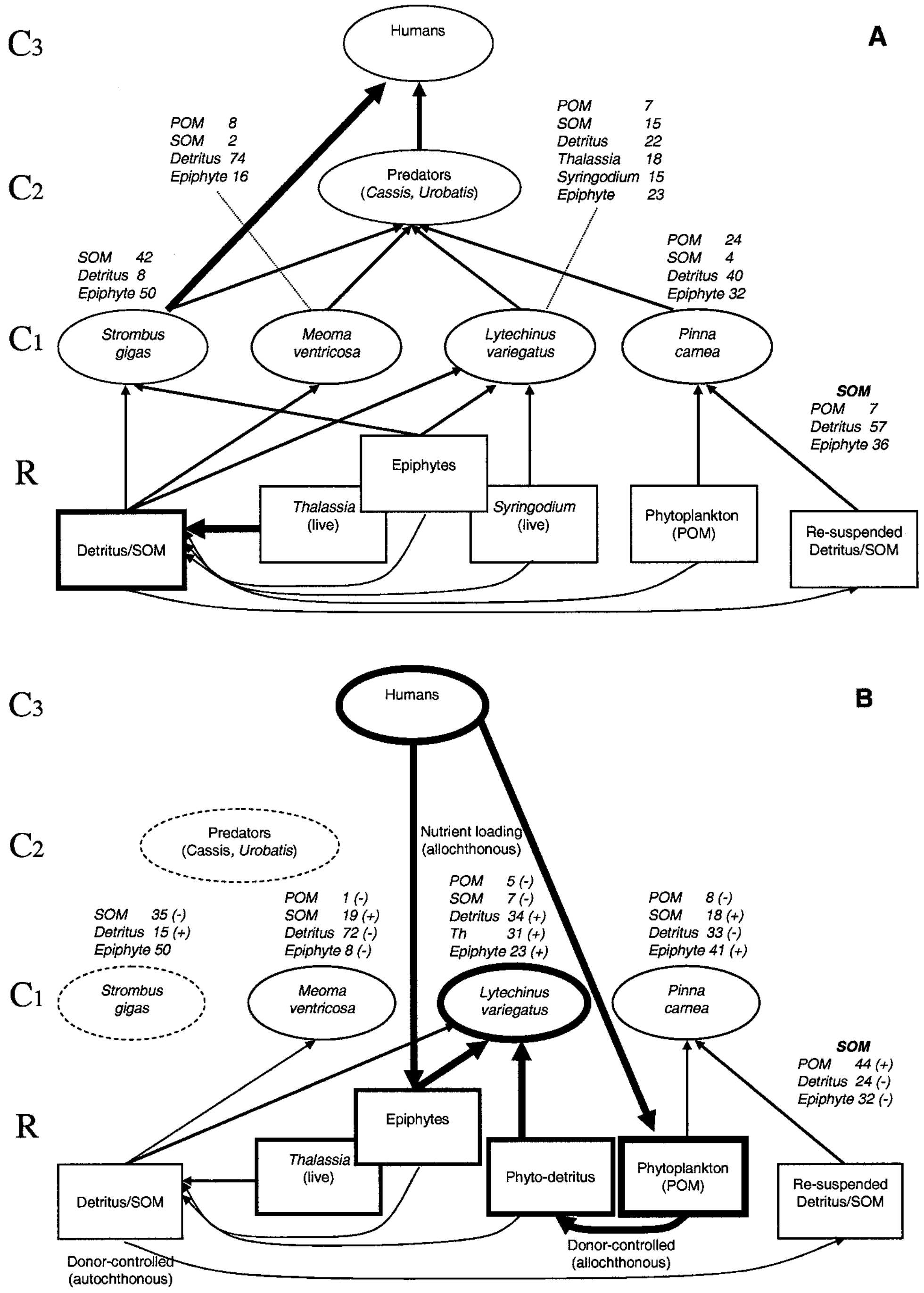

Fig. 5: Low, site 1 (A), and high, site 2 (B), nutrient enriched Caribbean seagrass food webs. Polygons, resources (R); ovals, consumers (C); arrows, energy flow. Weights of symbols indicate relative abundance (poygons, ovals) and flow (arrows). Values associated with consumers are mean percent contribution to the diet, + and – symbols for B are changes in mean values from A. (see appendix 2 for details). Primary consumers represent various functional groups: *Strombus gigas* (specialists); *Lytechinus variegatus* (generalists); *Meoma ventricosa* (deposit feeders); *Pinna carnea* (suspension feeders).

Appendices

Appendix 1: Mean $\delta^{13}C$ and $\delta^{15}N$ (± 1 se) for resources, primary producers, primary consumers and secondary consumers at site 1 (Jaragua) and site 2 (Barahona), Dominican Republic. N = sample size. Paired t-test results (site 1 vs. site 2): * $P < 0.05$; ** $P < 0.0005$; ns = not significant. POM (particulate organic material), SOM (sediment organic material)

					paired t-tests (1 vs. 2)	
Material	**Site**	**$\delta^{13}C_{vpdb}$**	**$\delta^{15}N_{air}$**	**n**	**$\delta^{13}C$**	**$\delta^{15}N$**
Resources						
POM (1 m below surface)	1	-30.9 ± 0.7	6.8 ± 2.0	2	ns	ns
	2	-31.0 ± 0.7	6.0 ± 0.5	2		
SOM	1	-11.9 ± 0.4	-1.2 ± 0.3	2	**	ns
	2	-20.5 ± 0.2	-0.6 ± 0.5	2		
detritus	1	-8.6 ± 0.2	-0.3 ± 0.4	6	ns	**
	2	-9.4 ± 0.2	3.1 ± 0.3	4		
1° Producers						
Thalassia testudinum	1	-8.5 ± 0.3	0.9 ± 0.0	4	ns	**
(turtle grass)	2	-8.7 ± 0.1	3.5 ± 0.1	4		
Syringodium filiforme	1	-4.5 ± 0.4	0.6 ± 0.3	5	n/a	n/a
(manatee grass)	2	n/a	n/a			
epiphytes (seagrass)	1	-13.3 ± 0.6	0.6 ± 0.2	5	ns	**
	2	-14.4 ± 0.0	4.4 ± 0.1	6		
1° Consumers						
Strombus gigas	1	-12.4 ± 0.3	1.7 ± 0.0	12	*	**
(queen conch)	2	-15.8 ± 0.5	5.9 ± 0.3	5		
Strombus costatus	1	-12.7 ± 0.2	1.4 ± 0.4	5	ns (0.07)	*
(milk conch)	2	-14.4 ± 0.5	6.9 ± 0.3	4		
Lytechinus variegatus	1	-11.1 ± 0.7	2.5 ± 0.2	8	ns	**
(variegated sea urchin)	2	-12.2 ± 0.3	6.6 ± 0.3	9		
Tripneustes ventricosus	1	-10.8 ± 0.6	2.7 ± 1.1	6	ns	**
(West Indian sea egg)	2	-11.0 ± 0.6	7.9 ± 0.8	8		
Meoma ventricosa	1	-10.9 ± 0.2	2.7 ± 0.3	5	*	**
(red heart urchin)	2	-12.2 ± 0.3	5.8 ± 0.1	5		
Oreaster reticulatus	1	-7.2 ± 0.8	1.1 ± 0.3	4	ns	*
(cushion sea star)	2	-9.3 ± 0.9	5.0 ± 0.3	4		
Pinna carnea	1	-15.6 ± 0.1	3.3 ± 0.3	4	*	*
(pen shell)	2	-15.1 ± 0.0	6.2 ± 0.2	4		
2° Consumers						
Urobatis jamaicensis	1	-12.7 ± 0.1	6.2 ± 0.04	2	ns	ns
(yellow stingray)	2	-11.4 ± 0.08	11.24 ± 0.8	3		
Pseudupeneus maculatus	1	-14.4 ± 1.1	6.3 ± 0.3	5	ns	ns (0.07)
(spotted goatfish)	2	-13.5 ± 2.1	9.2 ± 0.7	2		
Astropogon. stellatus	1	-12.7 ± 0.7	5.2 ± 0.2	5	ns	*
(conchfish)	2	-12.1 ± 0.2	9.0 ± 0.4	2		
Pleuroploca gigantea	1	-9.4 ± 0.9	5.4 ± 0.4	4	n/a	n/a
(Florida horse conch)	2	-12.4	12.1	1		
Cassis sp.	1	-10.1 ± 0.6	5.4 ± 0.2	4	n/a	n/a
(helmet shell)	2	n/a	n/a			
Murex sp.	1	-11.3	6.7	1	n/a	n/a
	2	-12.3 ± 0.4	9.6 ± 0.9	4		

Appendix 2: Mixing model results for consumer tissues based on δ^{13}C and corrected δ^{15}N. Statistics include mean, standard deviation and 1 – 99 percentile ranges. No data indicates resources not readily available to that particular consumer.

Consumer	**Site**	**Statistics**	**POM**	**SOM**	**detritus**	***Thalassia***	***Syringodium***	**epiphytes**
Strombus gigas	1	mean		42.1	7.9			50
		SD		9.2	4.2			6.9
		1 - 99 %ile		25 - 59	0 - 17			37 - 63
	2	mean		34.8	14.8			50.5
		SD		2.3	3.5			5.3
		1 - 99 %ile		31 - 39	7 - 21			41 - 60
Lytechinus variegatus	1	mean	7.1	15.5	21.8	18.5	14.6	22.6
		SD	3.4	9.7	16.5	13.2	9.9	16.3
		1 - 99 %ile	0 - 14	0 - 38	0 - 66	0 - 52	0 - 40	0 - 62
	2	mean	5.2	6.9	33.5	31.3		23.1
		SD	3	3.8	20.8	19.1		15.3
		1 - 99 %ile	0 - 11	0 - 15	0 - 78	0 - 72		0 - 57
Meoma ventricosa	1	mean	8.2	1.5	74.2			16.1
		SD	2.5	1.5	9.9			12.8
		1 - 99 %ile	1 - 12	0 - 6	45 - 88			0 - 53
	2	mean	1.2	19.3	71.4			8.0
		SD	1.2	2.6	4.3			6.1
		1 - 99 %ile	0 - 4	15 - 25	61 - 79			0 - 22
Pinna carnea	1	mean	24	4	39.9			32.2
		SD	4.5	3.2	17.1			22.6
		1 - 99 %ile	14 - 31	0 - 12	2 - 67			0 - 83
	2	mean	7.7	18	33.3			41.0
		SD	4.7	3.5	17.7			24.3
		1 - 99 %ile	0 - 17	11 - 25	1 - 64			0 - 86

GENERAL CONCLUSIONS

"Because he can create his own micro-environment in the way of clothing and houses, and because of his ability to build transport to take him from one end of the Earth to another, he has managed to colonize most of the planet. The development of language, then of writing, combined with education, have enabled him to establish cultural traditions, all of them developed and widened by succeeding generations. Modern science has played a major role in man's recent development, opening still wider horizons, and giving him a frightening power over all other life on Earth." This quote describing *Homo sapiens* appears as the last paragraph of the *Larousse Encyclopaedia of the Animal Kingdom*, first published in France in 1969, and has been a part of my personal library since childhood. The impact of this paragraph is at once an illustration of the incredible achievements a single, quite recently evolved, species has made and at the same time clearly states the extraordinary danger this same species represents to all organisms and the irreplaceable life-support system which they combine to create. Modern science must now play a key role in addressing the fundamental changes *Homo sapiens* have caused to our "life-support system" as no other place may serve as such.

It is then in the understanding and defence of this "life-support system" that I embarked on this thesis. Although many threats exist due to the increasing presence of humans on the earth, this treatise has focused on the chronic effects of nutrient enrichment disturbance (i.e. eutrophication) within shallow-water, macrophyte-dominated communities of the Caribbean. These systems represent important pools of global biodiversity which, in a relatively pristine state, yield a number of ecosystem services including many that benefit our species directly. Eutrophication is considered by many as one of the most significant threats to coastal marine systems and has been the focus of extensive research in a number of systems. However, I have also provided insight into the consequences of losses in trophic heterogeneity (i.e. trophic level diversity) and associated life history strategies as well as an examination of successional patterns in light of natural (e.g. hydrodynamics) and anthropogenic (e.g. nutrient loading) disturbance regimes. Both of these supporting topics (i.e. trophic diversity, succession) are particularly relevant to consider in the overall understanding of the patterns and effects of disturbance in natural systems. Finally, the synergistic effects of multiple disturbance regimes and the possibility of alternate states is also highlighted and lies at the heart of continuing studies in modern, applied community and ecosystem ecology.

Specifically, I illustrated that certain disturbance regimes (e.g. hydrodynamics) may need to be viewed both as acute and chronic forms, revealing dynamic reversals of competitive hierarchies between functional groups (Chapter 1). This may suggest the potential existence of alternate states in natural systems that may be persistent and may run counter to previous concepts and examples of ecological succession. Such an understanding is critical given the significant levels of coastal development and associated changes in near shore habitats including mangroves, macrophyte beds, reefs and barrier islands. Then, I illustrated the importance of trophic heterogeneity in dampening trophic cascades that may result from anthropogenic disturbances in the context of both overgrazing (or physical removals) and nutrient loading disturbance (Chapter 2). The loss of such diversity, and associated life histories, may lead to simplified food webs and losses in ecosystem services as well as the emergence of "new" states which may again be persistent. Such stability may be a direct or indirect consequence of nutrient enrichment as it facilitates the production of new allochthonous and expanded autochthonous pools of opportunistic resources that may be utilized by stress-tolerant, flexible generalist consumers. I also illustrated interference competition between a ubiquitous, yet heavily exploited, specialist (conch, *Strombus gigas*) and a wide ranging generalist (urchin, *Lytechinus variegatus*). This interaction results in both the switch of urchins to secondary resources and the lowering of urchin condition factor in the presence of conch and adequate supplies of preferred detritus and may serve as a concrete example of the importance of trophic level heterogeneity. The conservation of such a dynamic may assist in the preservation of diversity enhancing seagrass and associated detritus from the overgrazing potential of generalist urchins. I also examined the distribution of producer and consumer functional groups across a gradient of increasing nutrient enrichment (i.e. increasing influence of human populations), which may be viewed as another example of "succession" (Chapter 3). With increasing enrichment, and associated over-harvesting, comes the rise in urchin populations, loss of autochthonous pools of seagrass detritus and decreased community diversity. Again, the importance of new allochthonous and expanded autochthonous pools of resources benefiting generalist consumers is highlighted. The illustration of such an anthropogenically induced "succession" may help identify: (1) areas where a precautionary approach to ecosystem and resource management should be undertaken and (2) areas that have perhaps reached a more critical level of disturbance that may require the application of more direct restoration actions. Finally, I used a detailed analysis of nutrient enriched and "pristine" seagrass food webs, using stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), to identify the source(s) of the resource subsidies (Chapter 4) to generalist consumers postulated in earlier chapters (Chapters 2, 3). The understanding and identification of such subsidies is important to the general understanding of food web dynamics and essential in light of the significant efforts directed towards restoration of a variety of systems after long-term impacts from anthropogenic nutrient enrichment, sedimentation and over-fishing.

The continued anthropogenic disturbance of coastal marine systems threatens to erode the many benefits we may derive from such areas, while at the same time such disturbances destroy any reasonable possibility of recovery, within reasonable timeframes, due to the existence and persistence of alternate states which we have helped to create. Again, in a practical sense there may be little difference between a slow recovery and an indefinite persistence despite the ongoing search for truly "theoretical" stable states. In a more holistic sense, the rapid erosion of the "natural order and disorder of things", through our short-term and catastrophic activities, may rapidly spill-over to other systems and systematically destroy the "life-support system" that has contained and facilitated our great radiation and achievements.

"The earth provides enough to satisfy every man's needs, but not every man's greed."

Mahatma Gandhi