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THE H. T. ODUM SYNTHESIS ESSAY

The Primacy of Top-down Effects in Shallow Benthic Ecosystems

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ABSTRACT: Individual scientists, scientific organizations, and government agencies have all concluded that eutrophication is among the most detrimental of all human activities in coastal ecosystems; very large amounts of funding have been earmarked to study the negative consequences of nutrient pollution. Most studies of eutrophication have been conducted long after the numbers and diversity of larger marine consumers were dramatically reduced by centuries of intense harvesting. It is now understood that these once abundant predators played pivotal roles in regulating ecosystem structure and function, and that the widespread overharvesting of large consumers can trigger indirect effects that alter species compositions in ways that are very similar to those reported to result from eutrophication. All of this suggests that we should reevaluate whether the many negative effects attributed to eutrophication are actually a result of nutrient additions or whether they may be the result of the indirect effects of dramatically altered coastal food webs. In this essay, we review experimental assessments of the degree to which changes in consumer abundances have indirectly altered the structure of benthic ecosystems in coastal waters, and on the relative importance of top-down and bottom-up effects on coral reefs, rocky shores, and seagrass meadows. We find that the evidence clearly indicates that indirect consumer effects are the primary drivers of coastal benthic ecosystem structure and function.

Introduction

OVERVIEW

In the past two decades, individual scientists, scientific organizations, and government agencies have all concluded that eutrophication is among the most detrimental of all human activities to coastal ecosystems (Nixon 1995; Bricker et al. 1999; Howarth et al. 2000; NAS 2000; NSF 2000). As a result, very large amounts of funding have been, and continue to be, earmarked to study the effects of eutrophication in coastal waters. Among the most compelling evidence of the negative consequences of eutrophication are recurrent and persistent periods of hypoxia and anoxia (Diaz and Rosenberg 1995; Rabalais and Turner 2001), frequent harmful algal blooms, and the overgrowth of seagrass meadows and coral reefs by macroalgae (Howarth et al. 2000). Most studies of nutrient pollution have been conducted long after the numbers and diversity of larger consumers were dramatically reduced by centuries of intense harvesting (Dayton et al. 1995, 1998; Pinnegar et al. 2000; Myers and Worm 2003; Pandolfi et al. 2005). We now know that the harvesting of large consumers, in many cases to functional extinction, can trigger indirect effects that result in altered species composition and abundance at several trophic levels, and can be very similar to those reported to result from eutrophication (Heck et al. 2000; Williams and Heck 2001). This suggests to us that the extent to which the negative effects attributed to the eutrophication of coastal waters are a result of nutrient additions, or whether they are due to the indirect effects of dramatically altering food webs, is unclear. In our opinion, the evidence, which we review below, strongly suggests that indirect consumer effects are often the primary drivers of coastal ecosystem structure and function.

Indirect effects, by their nature, are complex and difficult to identify. In part, this is because they include interactions among three or more species and are defined as "how one species alters the effect that another species has on a third" (Strauss 1991, p. 206). Indirect effects include a host of different interactions, including apparent competition, apparent mutualism-facilitation, exploitative competition, and most famously, trophic cascades (cf., Strauss 1991; Wootton 1994). The difficulty in recognizing indirect effects, along with the traditional focus of fisheries managers on changes in the populations of single species rather than on the indirect ecosystem effects of fishing, may have delayed study of the importance of the effects of losing apex predators from coastal waters. This delay in assessing the indirect consequences of removing large predators is somewhat surprising, given that predation is a fundamental process that has long been known to shape the structure of

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marine ecosystems (see Pauly and Watson 2005), and the primary means by which energy is transferred from primary producers to other trophic levels. There also is a large body of work that documents the strong effects of smaller sized predators on macroinvertebrates in coastal waters (e.g., see reviews by Peterson 1979 and Wilson 1990) and the well known literature on the indirect effects of predators in rocky intertidal and subtidal areas, including the papers of Connell (1961), Paine (1966), and Estes and Palmisano (1974).

It may also be that the importance of the indirect effects of removing large predators was overlooked by estuarine ecologists who spent much of their time evaluating the mediating effects of structured habitats on the foraging efficiencies of predators (e.g., seagrass meadows: Heck et al. 2003, salt marshes: Minello et al. 2003, mangrove forests: Sheridan and Hays 2003, and oyster reefs: Coen et al. 1999). Higher survival rates of juvenile finfish and shellfish and reduced foraging efficiencies of larger predators are among the most consistently found characteristics of estuarine nursery habitats (Beck et al. 2001), as are low survival rates of epifaunal organisms on unstructured sand and mud bottoms. Even though the present day effects of predation are probably greatly reduced from what they once were, these many studies leave no doubt that marine predators continue to determine species abundances, compositions, and habitat utilization patterns. Additional examples, some not yet supported by experimental evidence, are reviewed by Jackson et al. (2001), Dulvy et al. (2004), and Steneck and Sala (2005), but it remains true that most coastal ecologists continue to emphasize the primacy of bottom-up factors, most notably nutrient availability, in determining the dynamics of coastal ecosystems (Howarth et al. 2000; LaPointe et al. 2005; Hauxwell et al. 2006).

Although it is understood by many investigators that both top-down and bottom-up factors can act in concert to determine the structure and function of coastal ecosystems (Lotze et al. 2006), experimental assessments of the relative importance of these two factors remain rare. Our view is that estuarine ecologists have been so heavily focused on bottom-up factors as regulators of ecosystem structure and function that the very large simultaneous effects that consumers can have on estuarine ecosystems remain unappreciated. Whatever the reason, our goal here is to summarize the results of recent experiments and meta-analyses of experimental studies that have assessed the strength of indirect consumer effects. We also evaluate an additional set of studies that compared the relative importance of top-down and bottom-up factors on benthic food webs in coral reef, rocky shore, and seagrass systems. Seagrass meadows are emphasized because we know them best, and because their global decline and their clear connection to a vast array of important ecosystem services (Orth et al. 2006) have made them a subject of many recent studies. The final section of this essay contains recommendations for research projects that will allow a better understanding of how anthropogenic manipulations of consumers can fundamentally alter estuarine ecosystems.

Data Sources and a Caveat

We focus our discussion on studies that relied on manipulative experiments because we believe that experimental evidence is the only conclusive way of evaluating the magnitude of indirect effects and of quantifying the relative importance of top-down and bottom-up factors on coastal ecosystems. Many papers that report observational or correlative evidence are not considered here, even though they contain important information. We also chose not to discuss in detail the most familiar examples of cascading trophic effects, those involving kelp forests, sea urchins and sea otters, and sea urchins, algae, and coral reefs, either because they are included in the meta-analyses or because they already appear in most basic marine biology textbooks (e.g., Valiela 1995; Nybakken 2000; Levinton 2001).

Before proceeding, we should make it clear that we share the opinions of Dayton et al. (1995), Jackson et al. (2001), and Steneck and Sala (2005) who have argued that virtually all of the published predation studies have been carried out under conditions that are fundamentally different from those that existed when most predator–prey relationships evolved. This is because humans have removed extraordinary quantities of large consumers from the world's coastal oceans, so that many are ecologically extinct, and some have been so for as long as several hundred years (see examples in Dayton et al. 1995, 1998; Jackson et al. 2001; Myers and Worm 2003; Steneck and Sala 2005). Because we believe that most coastal ecosystems are now devoid, or nearly devoid, of apex predators, as well as many mid and lower order consumers (Pauly et al. 1998), it is unlikely that any of the published studies were conducted in ecosystems whose species composition was similar to that prior to human intervention. In most instances we can only speculate on the importance of apex predators in estuarine and coastal ecosystems, although it is very likely that top-down pressure on estuarine and coastal food webs is much lower than it once was (Pauly and MacClean 2003). Many intermediate predators remain (perhaps in recently elevated numbers), because of release from control by apex predators (see Steneck et al. 2004) and their abundances and compositions have been manipulated in both intended and unintended ways by commercial interests and government agencies with jurisdiction over these resources (Pauly and MacClean 2003). It is with these caveats that we evaluate the evidence for consumer-driven indirect effects, and the relative importance of nutrient supplies and consumers on benthic ecosystem structure and function.

Evidence for Very Strong Indirect Consumer Effects on the Marine Benthos

The Shurin et al. (2002) paper is significant because it sheds light on the relative strength of consumer effects in marine ecosystems. The authors compared the strengths of trophic cascades documented in six very different types of food webs: lentic, marine and stream benthos, lentic and marine plankton, and terrestrial grasslands plus agricultural fields. They included 102 studies in their analysis and found that the strongest evidence of trophic cascades came from studies done in marine benthic systems (Fig. 1). That is, manipulations of the density of benthic predators produced stronger indirect effects on primary producers, via shifts in herbivore abundance, than did predator manipulations in terrestrial, marine or lake planktonic, or stream or lake benthic systems. A more recent meta-analysis by Borer et al. (2004), which included the 102 studies used by Shurin et al. (2002) plus 12 others, also found that trophic cascades were strongest in the marine benthos. While these meta-analyses were based primarily on rocky intertidal studies, they clearly demonstrate that indirect consumer effects are common and strong in marine benthic food webs. This also seems to be true in salt marshes where recent studies (Silliman and Bertness 2002; Silliman et al. 2005) have suggested that fisheries-induced reductions in blue crab (*Callinectes sapidus*) density have allowed one of their main prey items, herbivorous littorine snails (*Littoraria irrorata*), to increase their abundance dramatically. This increase in snail density in turn led to increased grazing pressure on, and reductions in, cordgrass (*Spartina alterniflora*), much in the same way that reductions in sea otters (*Enhydra lutris*) released urchins (*Strongylocentrotus purpuratus*) from predatory control, and once released, the urchins decimated kelp (*Macrocystis pyrifera*) forests (see review by Estes 2005).

Another opportunity to evaluate evidence on the indirect effects of manipulating higher trophic level predators comes from comparisons of food web interactions in replicated no take Marine Protected Areas (MPAs) and nearby fished sites. The establishment of MPAs represents a form of whole

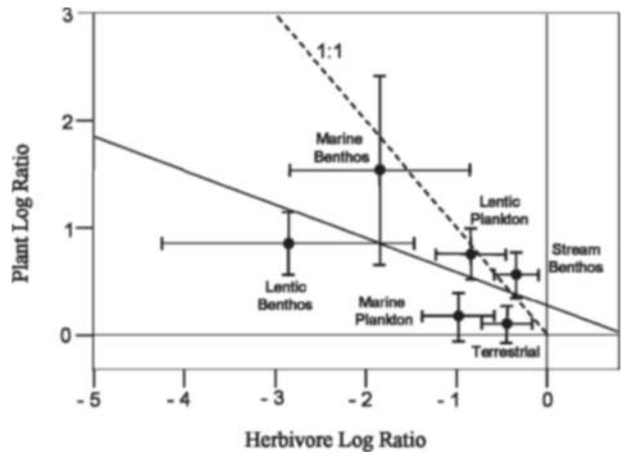

Fig. 1. Effect size of predators, as measured by the log ratio of herbivore and plant density in the presence and absence of predators (± confidence interval). The effect of predators is significant if the confidence interval does not overlap zero. Predators with relatively little effect on lower trophic levels are found on the lower right, while those with large effects (e.g., marine benthos) occur on the upper left. The linear regression relating plant and herbivore effect sizes is shown by the solid line and the 1:1 relationship is shown by the dotted line (source: Shurin et al. 2002).

ecosystem manipulation (Estes and Peterson 2000) in which enforcement of no take regulations can allow the recovery of overfished higher order consumers (e.g., Halpern and Warner 2002; Russ and Alcala 2004; McClanahan and Graham 2005). The restoration of higher trophic levels, when studied in conjunction with nearby reference (fished) areas, provides the opportunity to assess the effects of once diverse assemblages of higher order consumers on lower trophic levels.

Evidence of strong consumer effects on lower trophic levels in MPAs has been mixed, with some investigators finding strong evidence of cascading indirect effects on lower trophic levels while others have not. For the most part, these cascades have been found in structurally simple food webs where slow moving invertebrates (e.g., sea urchins) are the key conduits for the transfer of primary production to higher order consumers (e.g., McClanahan 1998; Shears and Babcock 2003). When the key trophic intermediates are fishes and species richness is greater, trophic cascades seem to be diffuse (Jennings and Polunin 1997; Jennings and Kaiser 1998; Mumby et al. 2006). Perhaps this is because high diversity systems contain more omnivores and greater amounts of dietary overlap. Trophic cascades do occur in high diversity MPAs (McClanahan 2005), and some of the best examples of dramatic indirect effects of diverse assemblages of higher order consumers are the MPA studies of McClanahan and his colleagues in eastern Africa (McClanahan 1998). In this work, the presence of large and diverse assemblages of fishes controlled large-scale habitat distributions by consuming large numbers of sea urchins, reducing rates of coral reef erosion from urchin feeding and preventing replacement of reefs by seagrasses (McClanahan and Kurtis 1991). Such findings are commonplace worldwide for coral reefs within MPAs.

The Relative Importance of Top-down and Bottom-up Factors in Coastal Waters Coral Reefs and Rocky Intertidal Systems

A growing number of investigators have evaluated the effects of different types of consumers versus nutrient supplies on algal biomass, and concluded that the effects of consumers are greater than, or equal to, those of nutrients. Grazing has been found to have a greater effect on the biomass of macroalgae on coral reefs than nutrient enrichment by several teams of investigators (Larkum and Koop 1997; Miller et al. 1999; Koop et al. 2001; Szmant 2002; McManus and Polsenberg 2004). While no meta-analysis of the relative importance of top-down and bottom-up forces on macroalgal abundances on reefs has been published, and there is disagreement on the experimental methods used to manipulate nutrients on reefs (see Littler et al. 2005), the preponderance of the evidence favors both strong and concomitant consumer and nutrient effects on the abundance of reef algae.

On rocky shores, Hillebrand et al. (2000) found that benthic algal biomass was determined by strong and balancing effects of amphipod and gastropod grazing and nutrient delivery. Worm et al. (2000) also found that invertebrate grazers were able to buffer the effects of moderate nitrogen enrichment on algae in the western Baltic Sea. Another recent meta-analysis provides further evidence in support of the important roles that both consumers and nutrients play in controlling algal abundance. In an analysis of 54 marine benthic studies that manipulated both herbivore pressure and nutrient loading, Burkepile and Hay (2006; Fig. 2) found that both produced significant effects, but that decreasing herbivore abundance had stronger effects on benthic marine macroalgae than did increasing rates of nutrient loading.

The papers reviewed above constitute a large body of evidence that includes most of the experimental work that has been done. They show quite clearly that benthic consumers often have very large effects on their food supplies, as well as indirect effects on community composition, and that these effects are as large, and often larger, than those of nutrients. Taken in its entirety, this literature suggests that the accumulation of plant biomass in shallow benthic habitats is more likely to be controlled by consumer effects than by nutrients.

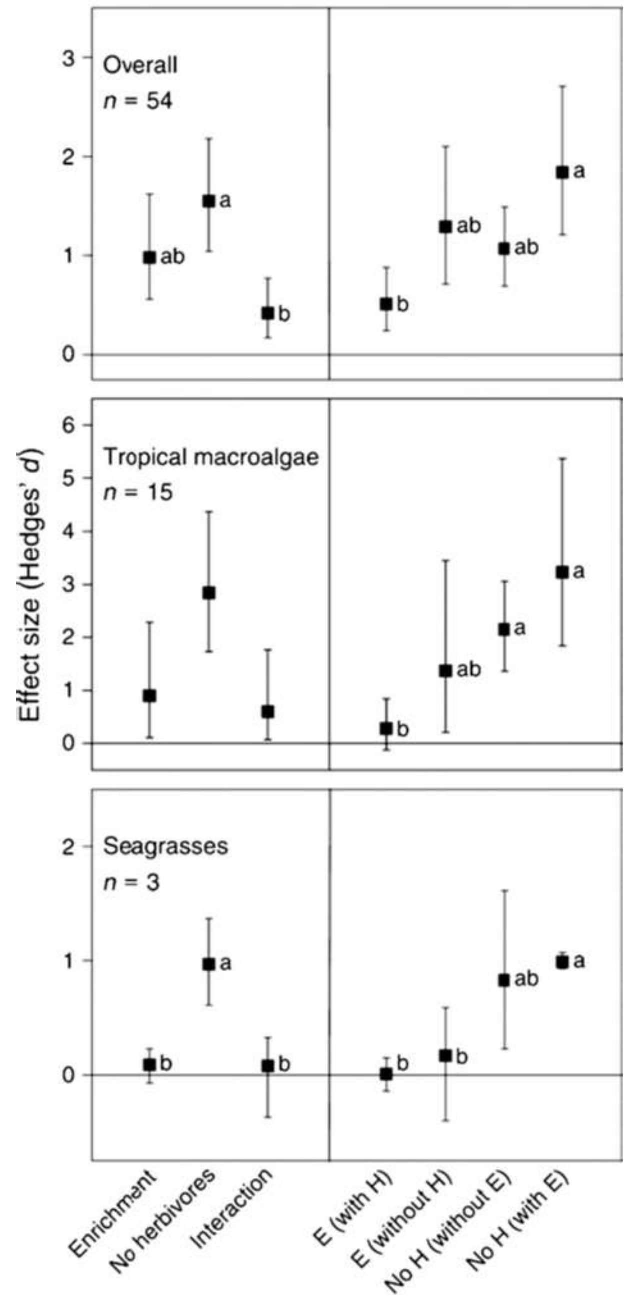

Fig. 2. Results of meta-analyses on mean and individual effects (left panel and right panel, respectively) for all primary producers, tropical macroalgae, and seagrasses from Burkepile and Hay (2006). Effect sizes are Hedges' $d \pm 95\%$ confidence intervals. Effects are significant ($p < 0.05$) if confidence intervals do not overlap 0. A positive d indicates an increase and a negative d indicates a decrease in primary producer abundance. Different lowercase letters designate differences among categories within an analysis as based on 95% confidence intervals, i.e., data points with different letters do not have overlapping confidence intervals. Graphs with no letters had no significant differences. Note the consistent pattern of greater effect size in the no herbivore treatments than in the enrichment treatments.

SEAGRASS MEADOWS

A prevailing view, which is part of the overall concern about nutrient enrichment, is that the increasing eutrophication of bays and estuaries has indirectly triggered global reductions of seagrass meadows via the overgrowth of seagrasses by the nutrient-induced proliferation of fast-growing algae (Duarte 1995; Bricker et al. 1999; Howarth et al. 2000; NAS 2000; Hauxwell et al. 2001). This explanation is most often proposed to account for the loss of seagrasses in North America (Orth and Moore 1983; Neundorfer and Kemp 1993; Short et al. 1995; Tomasko et al. 1996), Europe (Giesen et al. 1990; den Hartog 1994), and Australia (Cambridge and McComb 1984; Shepherd et al. 1989). An important point is that, for the most part, these studies were conducted in the absence of consumers. As noted by Heck et al. (2000) and Heck and Valentine (2006), when algal grazers (primarily mesograzers and some small herbivorous fishes) were included in study designs, grazing effects always explained at least as much, or more, of the variance in algal abundance than did nutrient enrichment (Neckles et al. 1993; Williams and Ruckelshaus 1993; Lin et al. 1996; see summaries in Valentine and Duffy 2006; and Heck and Valentine 2006). Nixon et al. (2001) summarized their work in mesocosms over a span of many years and reported that there were no significant increases in epiphyte biomass following nutrient enrichment, although they did observe changes in epiphyte composition.

In aggregate, results from these experimental studies clearly showed that mesograzers most often controlled the abundance of epiphytes, even in enriched conditions, a conclusion clearly at odds with the paradigm of nutrient-enrichment based seagrass decline summarized by Duarte (1995) and many others (Bricker et al. 1999; Howarth et al. 2000; NAS 2000; Hauxwell et al. 2001). These results are consistent with the hypothesis that top-down control, via cascading trophic effects like those associated with overharvesting large predators (Jackson et al. 2001), has important consequences for the flora and fauna of seagrass meadows (Heck et al. 2000; Heck and Valentine 2006). This hypothesis was further supported by a meta-analysis (Hughes et al. 2004) of the results of the studies cited above, along with all others that reported experimental results. Hughes et al. (2004) found that among the studies that compared the relative effects of nutrients and grazers on epiphytic biomass on seagrass leaves, grazers were a key determinant of the extent to which epiphytes overgrew living seagrass leaves. As they put it "The positive effects of epiphyte grazers were comparable in

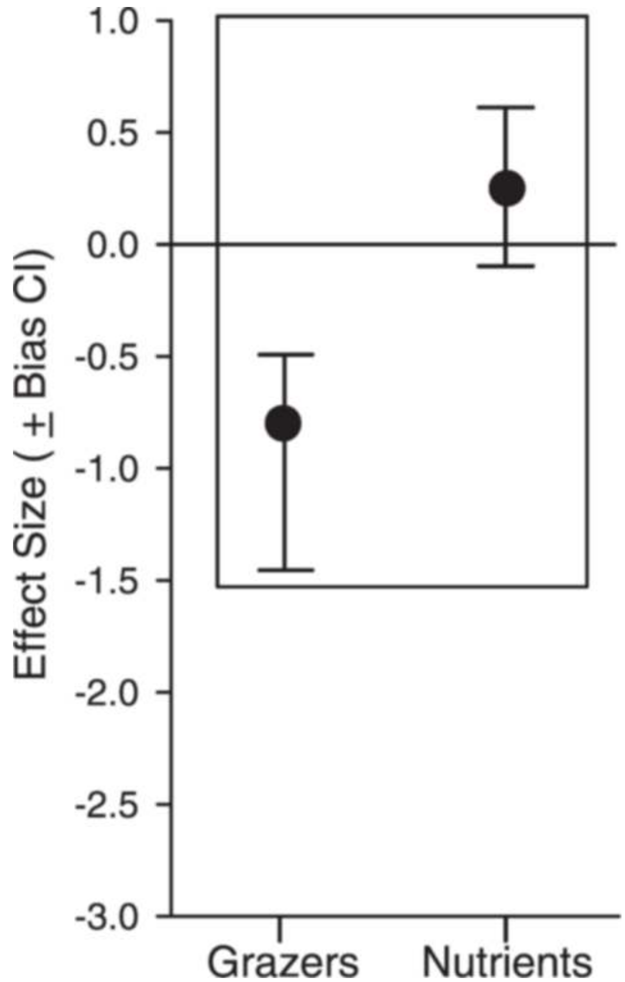

Fig. 3. The relative effect of grazers and nutrients on epiphyte biomass growing on seagrass leaves. Note that the magnitude of the effect of removing grazers is significantly greater than that of the nutrient addition effect (source: Hughes et al. 2004).

magnitude to the negative impacts of water column nutrient enrichments, suggesting that the 2 factors should not be considered in isolation of each other." (Hughes et al. 2004, p. 87). Their paper (see Fig. 3) actually showed that consumer effects were greater than those of nutrients and explained more of the variance in algal biomass than their cautious statement reflected. At locations where epiphyte loads on seagrass leaves are large, it seems to us that the most important questions to ask are why aren't grazers controlling epiphytic algae or what happened to the grazers (Heck and Valentine 2006).

A recent study of shoalgrass (*Halodule wrightii*) meadows in the Gulf of Mexico (Heck et al. 2006) found significant consumer and nutrient effects on seagrasses, although there were fewer consumer effects and more nutrient effects than in our previous study (Heck et al. 2000). Because epiphyte proliferation did not occur in nutrient enrichment treatments in this experiment, algal overgrowth could not explain the negative effects of nutrient loading on seagrass biomass that we found. Nutrient loading produced nitrogen-rich shoalgrass leaves, and this high-quality food stimulated increased pinfish (*Lagodon rhomboides*) herbivory. Elevated pinfish consumption of the enriched shoalgrass then resulted in the decline of seagrass biomass in enrichment treatments. These unexpected results are similar to those of Williams (1988), McGlathery (1995), and Goecker et al. (2005), who all observed that elevated nitrogen content in seagrass leaves triggered increased fish grazing, and they demonstrate that there is much more to learn about the interacting effects of nutrient supplies and the feeding patterns of consumers in seagrass meadows.

Changing Paradigms for Shallow Benthic Ecosystems?

Research on submerged aquatic vegetation in lakes in the United Kingdom has gone through a transformation that appears to be similar to what we have described for seagrasses. In British lakes, nutrients were first thought to be the driving force leading to the demise of rooted macrophytes (see Phillips et al. 1978). Jones and Sayer (2003) concluded that the key determinant of shallow water plant biomass was actually fish predation on invertebrates, which, through a trophic cascade, indirectly influenced the biomass of leaf periphyton and rooted macrophytes. While nutrient enrichment is an extremely important issue in coastal areas throughout the world, because of its association with phytoplankton and macroalgal blooms, so too are food web interactions, which must not be overlooked in future studies of eutrophication. The notion that top-down control is of primary importance in seagrass meadows worldwide requires further corroboration in other parts of the world (see below), but the evidence for this is abundant and growing (cf., Heck and Valentine 2006), and it comes with a number of applied implications (e.g., reducing nutrient inputs to coastal waters may not bring about full seagrass recovery if epiphyte grazers are artificially low in abundance). Evidence for the primacy of consumer effects in determining algal biomass is also growing stronger for coral reefs, kelp forests, and rocky shores, as discussed above, and we believe it likely that top-down factors will soon be generally acknowledged to be of primary importance in most marine benthic ecosystems.

Future Needs

There is a clear need to evaluate the generality of the results discussed above at sites beyond temperate North America, Europe, and Australia. We also need to determine more clearly the extent to which the findings of small scale studies conducted in the laboratory or in the field can be extrapolated to predict the relative effects of top-down and bottom-up factors at the ecosystem level, because most information on the effects of higher order consumers on lower trophic levels comes from experiments conducted at scales of one to tens of meters. Processes operating at such small spatial scales often differ from those operating at larger scales (Thrush et al. 1995; Crowder et al. 1997; Sih et al. 1998; Estes and Peterson 2000). Conclusions from small-scale experiments cannot safely be extrapolated to entire ecosystems without validation (Walters and Holling 1990; Eberhardt and Thomas 1991; Menge 1992; Carpenter 1998), and other approaches to evaluating the effects of larger, highly mobile, apex predators are needed. To date, large-scale manipulations (e.g., at the size of an embayment) of consumers and nutrients have not been conducted in coastal waters. Limnologists have learned a great deal by manipulating entire lake ecosystems (e.g., Schindler 1998; Carpenter et al. 2001), even though replication and controls are often difficult to include in such study designs. We feel strongly that marine and estuarine ecologists could benefit greatly from employing this approach.

We caution that most of the studies analyzed by Shurin et al. (2002) and Borer et al. (2004) manipulated only a single species of predator. Most food webs contain a diversity of consumers whose interaction strengths vary greatly, and their combined effects can be unpredictable and non-additive (Crowder et al. 1997; McCollum et al. 1998; Sih et al. 1998). There is a need to simultaneously manipulate multiple variables to better simulate conditions in nature and more realistically evaluate the relative importance of top-down and bottom-up factors. Prior studies have manipulated nutrients and usually only one type of grazer. This design should be expanded to manipulate multiple physicochemical variables (e.g., salinity, nutrients, and temperature), along with multiple combinations of grazers (Estes and Peterson 2000; Ibarra-Obando et al. 2004).

Additional Top-down and Bottom-up Questions

There are other questions about the operation of top-down and bottom-up processes that remain to be answered. If algal grazers prefer nitrogen-rich plants, as demonstrated experimentally for seagrasses by Williams (1988), McGlathery (1995), and Goecker et al. (2005) and for algae by Hemmi and Jormalainen (2002) and Boyer et al. (2004), how can nitrogen-rich filamentous green algae, which are characteristic of eutrophic waters, accumulate when grazers are present? One likely answer is that since most filamentous green algae are palatable to a wide range of grazers, persistent accumulations of green algae are only possible if there are few grazers present. This can easily be tested experimentally, using both nitrogen-enriched and unenriched algae with a variety of consumers.

Are there latitudinal differences in the stimulatory effects of elevated nutrient inputs on epiphytic algae (e.g., more negative effects in cold than warm climates because grazer abundance may not be able to catch up to algae that begin spring-time growth before animals in areas with short growing seasons)? This can be addressed by comparing the results of latitudinally distant studies, and this can be done simply by separating the studies in the meta-analyses discussed above by latitude.

Are there positive effects of nutrient enrichment on the consumers of algae with high nitrogen content and altered carbon:nitrogen:phosphorus ratios? Ecological stoichiometry predicts that elemental ratios of consumers will remain constant, despite the makeup of their food sources. To achieve this constancy, consumers must adjust their assimilation and excretion efficiencies in accord with the elemental composition of their food (Elser and Urabe 1999). Because food quality can play a major role in determining the growth and fecundity of consumers, we might expect positive effects on these factors in eutrophic waters containing nitrogen-rich algae. To date, we are not aware that this has been tested with coastal consumers.

Can chemically defended algae (e.g., red and brown algal species) become abundant on the surfaces of substrates (e.g., rocks, bivalve shells, or seagrass leaves) even in locations where grazing is intense? This could happen when fast-growing palatable algae (e.g., filamentous green algal species) are kept in check by grazers, which then allows slow-growing unpalatable species to proliferate. Drift algal mats of brown and red algae commonly found in North and Central American seagrass meadows may be an example, as may be the macroalgal accumulations often associated with eutrophic waters.

Trait-mediated Interactions

Until very recently, trait-mediated effects of predation on community structure and function have been virtually unexplored in marine environments (Dill et al. 2003). These nonlethal effects of predators on prey, primarily expressed through changes in prey behavior, can be as important as density-mediated (consumptive) predation in terrestrial and freshwater systems (see meta-analyses by Schmitz et al. 2004; Preisser et al. 2005). Marine examples that do exist include the work of Heithaus and Dill (2002; see also Heithaus et al. 2002), who have shown that predation threats by tiger sharks (*Galeocerdo cuvier*) altered the foraging behavior of bottlenose dolphins (*Tursiops aduncus*), such that they avoided the food-rich seagrass habits that are also favored by the tiger sharks. Dolphins trade off access to abundant food in the seagrass beds for increased survival rates. This trade-off benefits the fish as predation rates by dolphins are reduced (Heithaus and Dill 2002). In the New England rocky intertidal, trait-mediated effects were found to be as effective as density-mediated effects in regulating snail density that in turn regulated ephemeral green algal abundance in tide pools (Trussell et al. 2002, 2004). In the New England rocky subtidal, Freeman (2006) showed that small green sea urchin (*Strongylocentrotus droebachiensis*) grazing on macroalgae was significantly reduced in the presence of echinovorous sea stars (*Pycnopodia helianthoides*).

Dill et al. (2003) list a number of cases of both positive and negative effects of behaviorally-mediated interactions, one type of trait-mediated interactions (TMI) among marine organisms. While the number of existing cases is not large, TMIs are likely to be common in marine ecosystems, and can have important, unanticipated consequences for ecosystem structure and function (Dill et al. 2003).

Effects of Predatory Invasive Species

We briefly address the unanticipated, indirect effects that can arise from the introduction of nonnative consumers. This increasingly common phenomenon, with examples known in every type of shallow water habitat (Steneck and Carlton 2001) has led to some of the better known examples of marine trophic cascades. The introduction of the nonnative green crabs (*Carcinus maenas*) from Europe to the Gulf of Maine produced fundamental changes in the species composition and abundance of organisms in both subtidal flats and the rocky intertidal of New England (Steneck and Carlton 2001). Where periwinkles (*Littorina littorea*) are present, green crabs reduce periwinkle feeding by both direct and trait-mediated means, and this allows ephemeral green algae to proliferate. In the absence of green crab, periwinkles preferentially consume green algae and the result is dominance of the substrate by less palatable brown and red algae (Lubchenko 1978; Vadas and Elner 1992). Another location where nonnative consumers have had large effects on ecosystem structure and function is San Francisco Bay, where the Asian clam (*Potamocorbula* *amurensis*) has greatly altered phytoplankton species composition and abundance, improving water clarity that favors the proliferation of benthic plant species (Carlton 1999). Other examples include the effects of the nonnative ctenophore *Mnemiopsis leidyi* in the Black Sea (Malyshev and Arkhipov 1992) and the exotic seastar *Asterias amurensis* in Australia (Buttermore et al. 1994). In both cases the nonnative species had large effects on energy flow and food web structure (Steneck and Carlton 2001). The on-going process of marine introductions (Ruiz et al. 1997; Carlton 1999) constantly provides opportunities to investigate how commonly nonnative predators produce cascading effects that drastically change the food web structure of benthic ecosystems.

Plankton versus Benthos

We point out the surprising finding that there are relatively few cascading trophic effects in marine planktonic food webs (Micheli 1999). This was unexpected because the seminal work on the importance of trophic cascades was done on planktonic food webs in lakes (Carpenter and Kitchell 1993). Shurin et al. (2002) confirmed that in marine planktonic food webs, phytoplankton showed lower responses to predator removals than those in freshwater. Whether this lack of cascading effects reflects a fundamental difference between the planktonic systems of fresh and salt water, a difference between the marine planktonic and benthic systems, or whether the effects of removing consumers from marine planktonic food webs has attenuated strong cascading effects, is debatable. Stibor et al. (2004) and Duffy and Stachowicz (2006) suggest that apex predator losses often do cascade to marine phytoplankton, but whether the effect is positive or negative is determined by whether the food chain has three or four levels, which is a function of the cell size of the dominant phytoplankters. These authors suggest that because earlier studies (like those summarized by Micheli 1999), included results from both three and four link food chains, their effects cancelled out, leading to the incorrect conclusion that cascading effects in marine planktonic assemblages were weak (Duffy and Stachowicz 2006). There is much that remains to be explained about the organization of planktonic and benthic food webs in shallow coastal waters.

Conclusion

The papers reviewed here constitute a large body of evidence that includes most experimental work done on the indirect effects of altering consumer abundance, and on the relative importance of top-down and bottom-up factors on coral reefs, rocky shores, and seagrass meadows. It clearly shows, but only because manipulative experiments were used, that the indirect effects of benthic consumers are strong and much more widespread than most have believed. The cumulative effects of a diverse array of coastal consumers are, on average, as strong or stronger than the often reported effects of eutrophication. Taken in its entirety, this literature indicates that the accumulation of plant biomass in shallow benthic habitats is more likely controlled by consumer effects than by nutrients, and that indirect consumer effects are often the primary drivers of coastal ecosystem structure and function. We note that the implications of this conclusion for management are significant, as our analyses make clear that reducing nutrient input to coastal waters is unlikely to restore benthic habitats such as seagrass meadows or coral reefs if there have been pervasive alterations to food webs that have resulted in reduced mesograzer population sizes.

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