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# Eutrophication, Fisheries, and Consumer-Resource Dynamics in Marine Pelagic Ecosystems

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Anthropogenic nutrient enrichment and fishing influence marine ecosystems worldwide by altering resource availability and food-web structure. Meta-analyses of 47 marine mesocosm experiments manipulating nutrients and consumers, and of time series data of nutrients, plankton, and fishes from 20 natural marine systems, revealed that nutrients generally enhance phytoplankton biomass and carnivores depress herbivore biomass. However, resource and consumer effects attenuate through marine pelagic food webs, resulting in a weak coupling between phytoplankton and herbivores. Despite substantial physical and biological variability in marine pelagic ecosystems, alterations of resource availability and consumers result in general patterns of community change.

Increased nutrient loadings and fisheries exploitation are major human perturbations to marine ecosystems worldwide (1). Alteration of resource availability represents a "bottom-up" perturbation of marine ecosystems, whereas removal of consumer biomass through fishing represents a "top-down" disturbance. An understanding of how bottom-up and top-down processes influence the dynamics of marine communities is necessary for effective management of marine ecosystems in the face of environmental variability and multiple human impacts. However, it is difficult to determine the effects of resource availability and food-web interactions in open (pelagic), highly variable marine systems; most propositions are based on anecdotal evidence from catastrophic events such as El Niño years (2), fishery collapses (3), and the introduction of exotic species (4). To determine how marine pelagic ecosystems respond to variation in the quantity of resources and consumers, I conducted meta-analyses of data from a variety of experimental and natural systems and examined whether changes in the abundance of consumers (pelagic zooplanktivorous fish) cascade down marine food webs to affect

lower trophic levels, and whether changes in nutrient availability and primary productivity cascade up marine food webs to affect higher trophic levels.

To address these questions, I assembled data from experimental manipulations conducted in marine mesocosms and from long-term monitoring of open marine ecosystems. Experiments conducted in mesocosms eliminate open-system dynamics but represent controlled alterations of nutrient availability and food-web structure. In contrast, long-term monitoring of open marine systems documents patterns at realistic spatial and temporal scales. The first data set comprised phytoplankton and mesozooplankton (mostly herbivorous copepod crustaceans larger than 150 to 300  $\mu\text{m}$ ) data from marine mesocosm experiments where nutrient availability was manipulated by adding N compounds, or where food-web structure was manipulated by adding or removing zooplanktivorous fish or invertebrates (5). The second data set consisted of time series (7 to 45 years) of N availability (measured as the annual loading or as the average N concentration during winter months), primary productivity, and the biomass of phytoplankton, mesozooplankton, and pelagic zooplanktivorous fish for 20 open marine ecosystems (6).

For the mesocosm experiments, I quantified responses of phytoplankton and mesozooplankton to nutrient and food-web manipula-

tions by using the natural logarithm of the ratio between the mean value of the variable in mesocosms with carnivores (zooplanktivorous fish or invertebrates) or nutrients (inorganic N compounds) added and in unmanipulated, control mesocosms (7). Zooplanktivores caused significant decreases in mesozooplankton biomass, both in mesocosms with no N added (Fig. 1A) and in mesocosms enriched with N (Fig. 1B). Zooplanktivores caused an increase in phytoplankton biomass, but this trend was statistically significant only in systems that were also enriched with N (Fig. 1, A and B). Nitrogen addition caused similar and significant increases in phytoplankton biomass in mesocosms containing two (phytoplankton and zooplankton; Fig. 1C) or three trophic levels (phytoplankton, zooplankton, and zooplanktivores; Fig. 1D). Under either food-web configuration, nutrient addition did not affect mesozooplankton biomass (Fig. 1, C and D). The effects of the manipulations were not significantly correlated with either experiment duration or mesocosm size in zooplanktivore-manipulation experiments (8), and the effects were only weakly correlated with duration but not with size in nutrient-manipulation experiments (9). Therefore, these results are unlikely to be biased by the short duration or small mesocosm sizes used in most experiments.

For the 20 open marine ecosystems, I examined the cross-correlation between time series of nutrients, productivity, and biomass of different trophic levels using Spearman rank correlation (10). Theoretical models exploring the relations among resource availability, food-web structure, and biomass of different trophic levels predict patterns of biomass accrual along productivity gradients at equilibrium, that is, after transient effects have disappeared (11, 12). Because seasonal events such as upwelling and sudden increases in fish density from immigration or spring reproduction are transient effects, I used yearly values of productivity and biomass to approximate equilibrium conditions. Year-to-year fluctuations in mesozooplankton biomass were negatively correlated with zooplanktivorous fish ( $r = -0.22$ ; 95% confidence limits =  $-0.31$  and  $-0.12$ ;  $N = 19$ ), indicating that fish predation may control mesozooplankton biomass. In contrast, the correlation between mesozooplankton and

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phytoplankton was not significant ( $r = -0.07$ ; 95% confidence limits =  $-0.15$  and  $0.01$ ;  $N = 19$ ). This result may indicate that mesozooplankton does not control phytoplankton biomass, although a nonsignificant correlation could arise through mechanisms other than uncoupling between trophic levels. Negative correlations between zooplanktivorous fish and mesozooplankton and between mesozooplankton and phytoplankton were found in six systems, but they were not statistically significant (significance level  $\alpha = 0.05$ ) except for the correlation between zooplanktivores and mesozooplankton in one system, the subarctic Pacific (13). Thus, in pelagic marine ecosystems alterations of consumer abundance can cascade down food webs to affect phytoplankton biomass, but this effect is uncommon. Similarly, effects of changes in N availability and primary productivity rarely cascade upward to affect biomass of marine pelagic consumers. In general, N availability and primary productivity were positively correlated with phytoplankton biomass (Fig. 2). Correlations of nutrients and productivity with mesozooplankton and zooplanktivore biomass were not significant and showed no overall trend (Fig. 2). Positive, although nonsignificant, correlations between primary productivity and biomass of all trophic levels were found only in two systems (14).

Meta-analyses of data from mesocosm experiments and natural marine ecosystems indicated that pelagic marine food webs are

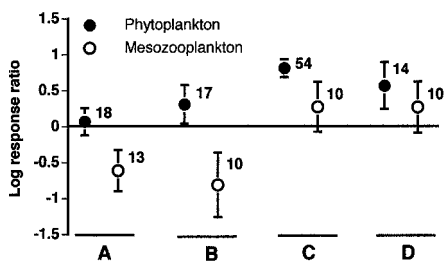
characterized by bottom-up control of primary producers (phytoplankton) through N availability and top-down control of herbivores (mesozooplankton) through predation by carnivores (zooplanktivorous fish). Both analyses indicated a weak coupling between primary producers and herbivores. Zooplanktivores tend to decrease mesozooplankton abundance, but the mesozooplankton commonly has no effect on the phytoplankton (Fig. 1). Conversely, increased N availability enhances primary producers but does not enhance the mesozooplankton (Figs. 1 and 2). In general, the effects of consumer-resource interactions do not cascade upward or downward through marine pelagic food webs.

The effects of carnivores (zooplanktivorous fish) on herbivores (mesozooplankton) and of nutrients on plants (phytoplankton), and the loose coupling between herbivores and plants, are pervasive. These patterns were observed at vastly different spatial (mesocosms to open ocean systems) and temporal scales (days to decades) and are similar to those found in syntheses of data from freshwater systems (15). The generality of these patterns indicates that similar mechanisms may underlie the dynamics of closed (freshwater) and open (marine) aquatic systems. Open, highly variable systems such as marine pelagic ecosystems may be regulated by local biological interactions similar to those occurring within naturally closed lake ecosystems or experimentally enclosed marine and freshwater systems.

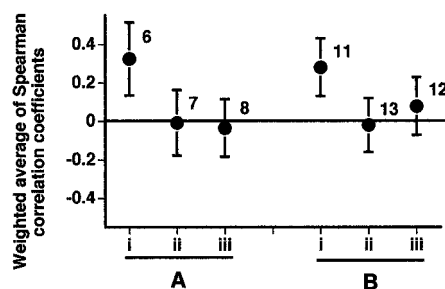
There are at least three biological mechanisms that might account for the observed weak coupling between primary producers and herbivores. First, coupling between trophic levels may be dampened by species interactions within the zooplankton; interference among zooplankton species may limit their population growth and hinder their top-

down effects on the phytoplankton (12). The trophic level abstraction used in many theoretical and empirical studies ignores the complexity of species interactions and thus may inadequately describe real food webs. Second, the efficiency of the transfer of primary productivity to higher trophic levels and the impact of herbivores on primary producers may depend on food quality, particularly the proportion of edible and inedible algae within the phytoplankton (16). Increased proportions of inedible algae frequently accompany increased productivity caused by anthropogenic nutrient enrichment (17). Finally, in open marine systems, advection or loss of nutrients and individuals from the focal system may dampen effects of local biological interactions and lead to an uncoupling between adjacent trophic levels (18). These mechanisms might act jointly to weaken primary producer-herbivore coupling in marine pelagic food webs.

These results have implications for management of marine ecosystems. First, the generality of a weak coupling of N loading and phytoplankton productivity with higher trophic levels (Figs. 1 and 2) implies that anthropogenic nutrient loading to coastal waters is unlikely to result in increased fish biomass, regardless of local physical and biological conditions and of the magnitude of nutrient enrichment. Phytoplankton production resulting from increased nutrient loading may be recycled within the plankton by microorganisms (19) or be lost from pelagic marine food webs when detritus settles to the ocean floor (20). Second, fluctuations in stocks of planktivorous pelagic fishes commonly affect zooplankton communities but rarely cascade through marine pelagic food webs to affect phytoplankton biomass. Thus, pelagic fisheries are expected to influence other ecosystem components, not directly targeted by the fishery, by affecting zooplankton biomass and food availability for other carnivores. However, it is unlikely that manipulations of marine food webs similar to those proposed for lakes (21) could be effective in controlling the response of primary producers to nutrient enrichment in coastal waters. Improved understanding of consumer-resource dynamics is critical both to predict the consequences of multiple anthropogenic perturbations to aquatic ecosystems and to develop sustainable management practices.



**Fig. 1.** Responses of phytoplankton and mesozooplankton to the addition of (A and B) zooplanktivorous fish or invertebrates and (C and D) inorganic N compounds to mesocosms containing pelagic marine communities. (A) Zooplanktivore addition was the only manipulation conducted in these experiments; (B) in addition to manipulating zooplanktivores, nutrients were added in identical amounts to both control and zooplanktivore mesocosms; (C) both control and nutrient-enriched mesocosms contained only phytoplankton and zooplankton; (D) both control and nutrient-enriched mesocosms contained phytoplankton, zooplankton, and zooplanktivorous fish or invertebrates. Means are averages of the log-transformed ratios of the mean treatment biomass divided by the mean in the controls, weighted by sampling variances. Bars are 95% confidence intervals. The number of experiments used to calculate each average log response ratio is indicated to the right of each mean.



**Fig. 2.** Correlation of (A) annual N availability (winter concentrations or loadings of inorganic N) and (B) mean annual primary productivity with (i) phytoplankton, (ii) mesozooplankton, and (iii) zooplanktivorous fish biomass in marine pelagic food webs. Means are averages of Spearman rank correlations between time series, weighted by sampling variances. Bars are 95% confidence intervals. The number of correlation coefficients averaged is indicated near each mean.

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  9. Log of the response ratio versus duration of experiments (in days),  $r = 0.23$ ,  $P = 0.09$ ,  $N = 54$  (without zooplanktivores), and  $r = 0.067$ ,  $P = 0.01$ ,  $N = 14$  (with zooplanktivores) for phytoplankton;  $r = 0.57$ ,  $P = 0.08$ ,  $N = 10$  (without zooplanktivores), and  $r = 0.08$ ,  $P > 0.10$ ,  $N = 10$  (with zooplanktivores) for mesozooplankton. Log of the response ratio versus mesocosm volume (in liters),  $r = -0.12$ ,  $P > 0.10$ ,  $N = 54$  (without zooplanktivores), and  $r = -0.35$ ,  $P > 0.10$ ,  $N = 14$  (with zooplanktivores) for phytoplankton;  $r = -0.09$ ,  $P > 0.10$ ,  $N = 10$  (without zooplanktivores), and  $r = -0.14$ ,  $P > 0.10$ ,  $N = 10$  (with zooplanktivores) for mesozooplankton. For all analyses, qualitatively similar results were obtained when short- and long-duration experiments were excluded.
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  14. Primary productivity versus phytoplankton: Kattegat,  $r = 0.42$ ,  $P > 0.10$ ,  $N = 10$ ; Middle Adriatic Sea,  $r = 0.38$ ,  $P > 0.10$ ,  $N = 6.3$ ; Primary productivity versus mesozooplankton: Kattegat,  $r = 0.2$ ,  $P > 0.10$ ,  $N = 5.3$ ; Middle Adriatic Sea,  $r = 0.41$ ,  $P > 0.10$ ,  $N = 9.4$ . Primary productivity versus zooplanktivores: Kattegat,  $r = 0.19$ ,  $P > 0.10$ ,  $N = 7.6$ ; Middle Adriatic Sea,  $r = 0.55$ ,  $P > 0.10$ ,  $N = 5.4$ .
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