

BEHAVIORALLY MEDIATED INDIRECT INTERACTIONS IN MARINE COMMUNITIES AND THEIR CONSERVATION IMPLICATIONS

LAWRENCE M. DILL,^{1,4} MICHAEL R. HEITHAUS,^{1,2} AND CARL J. WALTERS³

¹*Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada V5A 1S6*

²*Center for Shark Research, Mote Marine Laboratory, 1600 Ken Thompson Parkway, Sarasota, Florida 34236 USA*

³*Fisheries Centre, University of British Columbia, Vancouver, British Columbia, Canada V6T 1Z4*

Abstract. The importance of density-mediated indirect effects (e.g., keystone predators) in marine communities has been widely recognized. Behaviorally mediated indirect interactions (BMIs) may be equally important in marine systems, but have received relatively little attention. BMIs occur when a change in an “initiator” species causes a behavioral shift in a “transmitter” species that, in turn, affects a “receiver” species. BMIs between initiator and receiver species can be described by the ecological relationships between initiator and transmitter, and between transmitter and receiver (i.e., predator and prey, competitors, or no relationship), and the nature of the indirect effect on the receiver (i.e., positive or negative). We review published examples of BMIs in marine communities, showing that BMIs may create, enhance, ameliorate, or even reverse the sign of the direct interactions between species. Models that only include direct interactions or density-mediated indirect ones cannot predict some of these effects. BMIs are likely to be ubiquitous in marine communities and have important implications for both understanding community dynamics and managing these systems. A thorough understanding of BMIs is particularly important for conservation and management, as humans may play the role of an initiator, transmitter, or receiver of these effects in a variety of marine communities.

Key words: *apparent competition; apparent mutualism; behavior; conservation; facilitation; fisheries management; indirect effects; marine communities; predator–prey interactions.*

INTRODUCTION

Behaviorally mediated indirect interactions (BMIs) are a type of trait-mediated indirect interaction (TMII). They occur whenever a change in a property of some species (the “initiator”) causes a change in the behavior of a second species (the “transmitter”), and this change in the transmitter has an effect on a third species in the community, the “receiver” (definition and terminology after Abrams [1995]; see Fig. 1). The change in the transmitter species can occur either in evolutionary time (in which case we may speak of an adaptation), or in ecological time (in which case we are dealing with a type of phenotypic plasticity). Regarding the former, Abrams (1995) cites the example of an evolved antipredator trait conferring low risk, but reducing its possessor’s foraging effort or efficiency and its consequent impact on the food base. Although we are concerned here primarily with the shorter of the two time frames and mechanisms, experimental data that would allow us to draw a distinction are not always available.

As other contributors to this Special Feature have demonstrated, BMIs are common in terrestrial and

aquatic freshwater communities. They have been much less frequently reported in marine systems, even though other types of indirect effects, i.e., density-mediated interactions (DMIs) such as keystone predation and exploitation competition, are common there (Menge 1995). Based on explanations for BMIs, there is no particularly good reason to expect them to be less important in marine systems than in freshwater or terrestrial ones. Most likely they have simply been reported less often because interaction dynamics in marine systems are more difficult to document: it is logistically difficult to directly observe behaviors and spatial patterns in the ocean at scales where many BMIs are likely to develop. Yet the oceans cover 71% of the earth’s surface (representing proportionately much more habitable volume) and contain all but one of the known phyla and at least 15% of described species (Gaston and Spicer 1998). Furthermore, marine food webs appear to be at least as complex as those found elsewhere, and the pelagic webs tend to have more species of prey per predator (“generalization”) and more species of predator per prey (“vulnerability”) than other types (Schoener 1989). In addition, many marine invertebrates and fishes show ontogenetic shifts in trophic level, creating even more opportunities for interaction. Thus, there should be no shortage of examples of indirect interactions, including those that are behaviorally mediated.

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⁴ E-mail: ldill@sfu.ca

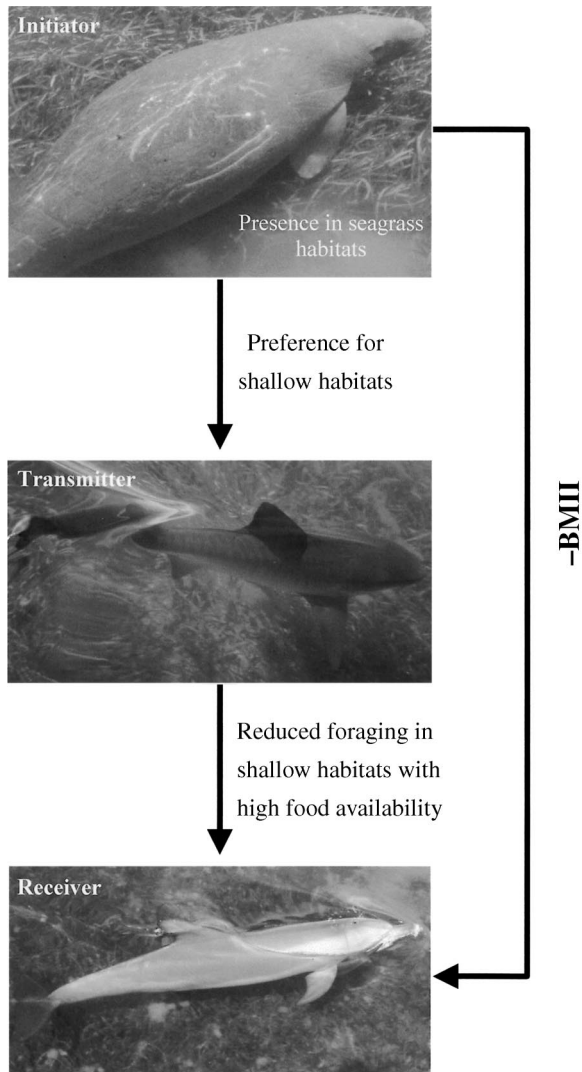


FIG. 1. An example of a behaviorally mediated indirect interaction (BMII). Such interactions occur when a change in an initiator species causes a behavioral shift in a transmitter species, which in turn affects a receiver species. BMII's may have positive or negative effects. In this example, the seasonal peaks in abundance of dugong and other tiger shark prey species, as well as their preference for shallow habitats result in peaks in tiger shark abundance in shallow habitats during summer. This, in turn, causes dolphins to reduce their use of shallow, productive habitats during foraging. Therefore, the presence of dugongs probably has a negative effect on dolphin food intake.

One of the goals of this paper is to provide some marine examples of BMII's from the literature and from the work of two of the authors (L. M. Dill and M. R. Heithaus) in a seagrass ecosystem in Shark Bay, Western Australia. In the course of that research, we became impressed with the potential role of BMII's in structuring marine communities and were stimulated to search the literature for other examples. In presenting them here, we hope to demonstrate how knowledge of

BMII's can contribute to improved understanding of species interactions, not only in undisturbed systems, but also in human-impacted ones, and thus contribute to improved theory and practice in conservation science, including fisheries management.

OVERVIEW OF TYPES OF BMII'S

BMII's can be usefully described with reference to the following criteria, where I, T, and R refer to initiator, transmitter, and receiver species, respectively:

- 1) the initial ecological relationship between I and T, which can take the form of predation, herbivory or parasitism (of I on R, or vice versa), competition, commensalism, mutualism, or neutralism;
- 2) I's actions that affect T, including the mere presence of I, changes in its density or spatial distribution (e.g., aggregation), or particular behaviors that it performs;
- 3) the behavior of T that is altered, including overall activity level, feeding, hiding, aggregation, or habitat use;
- 4) the initial ecological relationship between T and R (as in point 1); and
- 5) the effects on R, including altered food availability, habitat structure, or risk of predation (all of which could increase or decrease).

Even with this minimal set, there are many possible types of BMII, and we have not found examples of them all. However, they resolve into two major functional categories, namely: (1) those with a positive impact on R by I, or (2) those with a negative impact on R by I. By "positive," we mean an increase in access to food, survival, growth rate, foraging activity, etc., that is likely to result in an increase in equilibrium population size; by "negative," we mean the reverse. The label given to a particular type of BMII will depend on both the nature of the indirect effect (positive or negative) and the initial ecological relationship of I and R.

BMII'S IN MARINE ECOSYSTEMS

We now provide some marine examples of both positive and negative BMII's and the ways in which they come about, as well as some related phenomena.

Positive impact of initiators on receivers (facilitation)

"Competitor facilitation" refers to a situation whereby the presence of one species of predator (I), through its effect on the behavior of its prey (T), makes these prey more available to a competing predator species (R). Where this effect is reciprocal (no marine examples are known to us), we may refer to this situation as "apparent mutualism." In either case, it has the potential to reduce or even override exploitation or interference competitive effects between the predator species. An example of this type of BMII occurs in fish (spot, *Leiostomus xanthurus*) that are facilitated by the

presence of blue crabs (*Callinectes sapidus*). Crabs cause amphipods to climb up any available structures, thereby providing more food for the fish, and increasing the latter's survival (Martin et al. 1989). A second example comes from the rocky intertidal zone, where urchins (*Strongylocentrotus purpuratus*) avoid the asteroid *Pycnopodia helianthoides* by fleeing and climbing upon one another's backs. In doing so, urchins sometimes lose their grip and are swept by the waves into tide pools where they become food for sessile anemones (*Anthopleura xanthogrammica*) that otherwise would have little chance to feed upon them (Dayton 1973). Dayton (1973) even used this as an example of how the predictions of a model (in this case, of competition) may be met for entirely wrong reasons. This example shows how important it is to consider the role of BMIs if we hope to understand the processes structuring communities.

Many other examples of competitor facilitation are known. Schools of herring (*Clupea* and related species) form tight aggregations (these dense schools are often referred to as "balls") and rise to the surface in response to attacks from subsurface predators such as large fish, diving birds, and marine mammals (e.g., Ribic et al. 1997, Sharpe 2001). This behavior makes the fish vulnerable to aerial predators such as gulls, so an asymmetrical indirect interaction exists between subsurface (I) and aerial (R) predators. Other examples of this sort are discussed in later sections.

In many cases, there is no ecological relationship between I and R, but the behavior of T allows important BMIs. For example, when R is a prey species of T, rather than its predator, facilitation-type BMIs will occur anytime T trades off food intake against risk of predation, e.g., by foraging less in the presence of predator (I) cues or actively avoiding them through movement (numerous examples are summarized in Lima and Dill [1990]). When an animal trades off foraging and predation risk through behavioral means, its behavior is now necessarily set in an ecosystem context (a tri-trophic one at least). The species making the trade-off becomes a transmitter, and its predator (I) is bound to have indirect effects on T's prey (R), for example by reducing T's foraging rate. This is an important example of how behavioral ecology can inform community ecology. Trade-offs of this sort are quite common in marine systems, and are often odor mediated (an extensive review is provided by Kats and Dill [1998]), so these sorts of BMIs should be exceedingly common, despite relatively few known examples.

Posey and Hines (1991) provide a possible marine example of such a BMI (although the mechanism is not discussed). Grass shrimp (*Palaemonetes pugio*) move into shallow water to avoid predatory killifish (*Fundulus heteroclitus*), which results in increased survival of the shrimp's infaunal prey. This is in addition to any density-mediated indirect effect of the killifish,

caused by removal of the shrimp, and thus BMIs may enhance existing density-mediated effects.

The effects of T's altered behavior may also include a reduction in physical disturbance. For example, the presence of a predatory neogastropod (*Purpura pansa*) causes an herbivorous archaeogastropod (*Nerita scabricosta*) to avoid the area where the former are present. As a result, there is less disturbance of settling *Chthamalus* barnacle larvae and a consequent increase in their numbers (Garrity and Levings 1981). In addition, the reduced grazing by *Nerita* facilitates the growth of algae and littorine gastropods, creating multiple BMIs with the same I and T in this community.

Effects of I on the behavior of a competing T species can also cause facilitation-type BMIs. For example, competition from the bivalve *Rangia cuneata* causes the clam *Macoma balthica* to switch from suspension feeding to deposit feeding (Skilleter and Peterson 1994). Because it must now extend its siphon farther to feed effectively, this increases siphon loss to predatory juvenile spot. Thus, an increase in *Rangia* density should lead to an increase in spot and other siphon nippers such as pinfish (*Lagodon rhomboides*), although this facilitation effect has not been shown experimentally. Furthermore, the competitive impact of *Rangia* on *Macoma* will be exacerbated by this indirect effect.

Facilitation can even be created between two species through nonpredatory avoidance responses by T. For example, the presence of *Sargassum filipendulum*, an unpalatable brown alga, reduces the local foraging activity of the urchin *Arbacia punctulata* and thereby reduces its grazing mortality effects on *Gracilaria tikvahiae*, a more palatable red alga (Pfister and Hay 1988). Although the mechanism in this instance is not reported, such indirect positive effects might be fairly common whenever predators avoid patches with large numbers of unpalatable or unprofitable prey, thereby affording the more preferred prey a degree of protection by association.

In some situations, there may be a positive BMI by prey (I) on their predators (R). Such "predator facilitation" is most likely when a second prey species plays the role of T. For example, the presence of tuna (I) may cause dolphins (T) to aggregate around them (Au and Pitman 1986). The dolphins' behavior has a positive effect on human fishing success for tuna because fishing boats can encircle the dolphins when setting nets. One interesting aspect of this BMI is that although there is a positive effect of tuna on fishermen, there is an increase in the mortality rate of tuna.

These examples of facilitation represent only a fraction of the possible mechanisms by which such positive BMIs could arise. Although we are unaware of examples of other mechanisms, future research will undoubtedly uncover them.

Negative impact of initiators on receivers

As for facilitation, there are many ways in which negative BMIs may occur, and we have only identified examples of a few. "Apparent competition" refers to a situation in which I and R do not share food resources, but I has a negative effect on R through a shared predator (T); in the case of a BMI, it is the predator's behavior that is affected. Because removal of I leads to an increase of R, the species appear to compete even though they share no common resources. This situation may be unidirectional or reciprocal; only the former has been reported in a marine community. For example, the addition to experimental plots of the bivalve *Chama arcana* causes an aggregation response by predatory octopus (*Octopus bimaculatus*) and lobster (*Panulirus interruptus*), which increases the mortality rate on a number of sympatric gastropods, particularly *Tegula eiseni* (Schmitt 1987).

This is a case in which the receiver species suffers higher mortality as a result of I's effect on T's behavior. However, some R species may avoid direct mortality through behavioral means, such as changing their patterns of habitat use. We have discovered an example of this in a community of large marine vertebrates in Shark Bay, Western Australia. During the austral summer, dugong (*Dugong dugon*), sea snakes (primarily *Hydrophis elegans*), and sea turtles (loggerhead, *Caretta caretta*; green, *Chelonia mydas*) are abundant in Shark Bay (Heithaus 2001). This concentration of prey in summer attracts many tiger sharks (*Galeocerdo cuvier*), which concentrate their foraging in the shallow seagrass habitats preferred by their prey (Heithaus et al. 2002). In response, bottlenose dolphins (*Tursiops aduncus*) shift out of these fish-rich seagrass habitats in summer, moving to deeper channels where both fish prey and sharks are less abundant. In doing so, they give up food but increase their safety (Heithaus and Dill 2002). The BMI (see Fig. 1) is between the tiger sharks' primary prey (I) and dolphins (R), via the sharks (T). Although dolphins do not compete with other tiger shark prey for food, their distributions are negatively associated, giving the appearance of competition.

Sometimes a BMI may intensify a preexisting competitive interaction between I and R, e.g., between consumers that use different methods of foraging for a common prey. Thus, when clams (*Mya arenaria*; T) detect the presence of predatory red rock crabs (*Cancer productus*; I), they bury themselves more deeply (Zaklan and Ydenberg 1997), which probably reduces their availability to shorebirds (R), whose bill length limits how deeply they can dig (Zwarts 1996:62–66). This is an example of what has been called "behavioral resource depression" (Charnov et al. 1976).

As discussed earlier, trade-offs between food and predation risk by a transmitter often result in positive BMIs between a predatory initiator and a receiver two

trophic levels below. However, the converse of such effects may be common in ecosystems whose top predators (such as sharks) are depleted by a fishery. Reduction in predator numbers allows their prey (secondary predators) to forage with relative impunity and to have a greater impact on their own prey species. Thus, a reduction in one species can reduce the numbers of another species two trophic levels below. These are described as "takes three to tango" effects in EcoSim models (Walters and Kitchell 2001). Although these generally will be difficult to disentangle from density-mediated trophic cascades that can act in the same direction (for a more detailed discussion, see Walters et al. [1997]), behavioral changes are likely to exacerbate density-mediated effects.

Marine examples of other phenomena related to BMIs

BMIs are only one type of trait-mediated indirect interaction, and examples of other types have been reported in marine systems (e.g., Raimondi et al. 2000). Some of these look like BMIs at first glance, but may not stand up to detailed scrutiny. For example, *Macoma* clams whose siphons have been nipped by flatfish (juvenile plaice, *Pleuronectes platessa*) move upward in the substrate, becoming more vulnerable to shorebirds (de Goeij et al. 2001). Although this is indeed a behavioral response, it is forced on the clams, who need to reach the substrate surface to feed with their now shortened siphons. It may be more appropriate to think of this indirect interaction between fish and birds as being mediated by a change in morphology.

Behavior of another species may also mediate interactions between marine animals and abiotic characteristics of their habitat. For example, Menge et al. (1996) suggested that increased foraging by seastars at wave-protected sites was responsible for the higher per capita interaction strengths with their mussel prey observed there, but this is not a BMI as we have defined it.

IMPORTANCE OF BMIs

Understanding community dynamics

BMIs may be important in marine ecosystems for a number of reasons, and it therefore behooves marine community ecologists to be aware of them and their potential.

Firstly, BMIs can create or expand niches. Several of the BMIs that we have discussed have this effect. Thus, *Macoma* is made more available to fishes due to the presence of *Rangia* (Skilleter and Peterson 1997); foraging asteroids make urchins available to tide pool anemones (Dayton 1973); and whales and tuna drive fish upward to create otherwise unavailable foraging opportunities for marine birds (e.g., Ribic et al. 1997). The existence of the spatial converse of the last situation is also likely: pelagic predators are known to drive

the euphausiid scattering layer downward (e.g., Onsrud and Kaartvedt 1998), and in that way may provide food for benthic fishes such as rockfish (*Sebastes* spp.).

Secondly, BMIs can amplify trophic interactions. Thus, as we have described, crabs reduce clam availability to shorebirds through both exploitation (DMII) and behavioral changes in their common prey (Zaklan and Ydenberg 1997).

Thirdly, BMIs can counteract trophic interactions, leading to surprising, counterintuitive outcomes. An especially interesting example comes from the work of one of us (C. J. Walters) on modeling ecological energetics using the EcoSim package (Christensen et al. 2000). Because both tuna and seabirds feed on small schooling fish, simple models predict that removing tuna will lead to an increase in seabird numbers. However, removing tuna actually results in fewer seabirds when realistic BMIs are included in the models, because predatory attacks by large pelagic fish such as tuna cause movement of small schooling fish closer to the surface, making them more available to diving seabirds (Au and Pitman 1986, Ribic et al. 1997). Both artisanal and modern fishermen also benefit from this BMI by targeting seabird flocks to access the fishes beneath them (Parrish 1999).

Finally, BMIs can involve more than three species and may create behavioral cascades, analogous to trophic cascades, by affecting additional species that interact with the Receiver. The food–risk trade-off described earlier in the Shark Bay ecosystem is likely to result in such a behaviorally mediated cascade. When dolphins shift habitats in response to the presence of tiger sharks (a BMI between dugongs/turtles and dolphins), this undoubtedly has effects on the fish communities (prey of dolphins) in both habitats, and probably on species even farther down the food chain, although such effects have yet to be documented (Heithaus and Dill 2002). Something like this has also been hypothesized for the urchin, *Centrostephanus coronatus*. The crevice-seeking behavior of this invertebrate in response to predation risk from fish (the sheephead, *Pimelometapon pulchrum*) limits its foraging range and is thought to create intense competition for food and to result in a broad diet, thereby negatively impacting multiple prey species (Vance and Schmitt 1979).

Urchins also illustrate the point that the consequences of BMIs may be apparent even in the physical landscape. In the Caribbean and elsewhere, predation pressure from fishes and snails, such as the king helmet snail, *Cassia tuberosa*, causes long-spined urchins (*Diadema antillarum*) to remain in the cover of patch reefs during the day. The urchins only venture out at night, and then travel only a short distance from the reef, where they crop down the turtle grass (*Thalassia testudinum*), creating a halo effect (Ogden et al. 1973). Similarly, Bernstein et al. (1981) propose that the aggregation response of *Strongylocentrotus droebachiensis* (another urchin) to its crab predators produces dense

feeding fronts along the edge of kelp beds and leads to the creation of “barrens.” This is a case in which it is not certain that the urchin’s behavior is a short-term behavioral response to predation risk or a long-term adaptation; however, given the well-documented ability of urchins to detect the odor of their predators (see Kats and Dill 1998), the former scenario is not unlikely.

The increasing realization that BMIs may be important in communities of all sorts is part of a larger appreciation of the role of behavior in ecology more generally, and the marine realm specifically. Thus, Chapman (2000) recently argued that much more attention should be paid to flexible behaviors and their effects in intertidal habitats. Even such classical problems as intertidal zonation can benefit from a behavioral approach, once it becomes apparent that marine invertebrates are quite mobile and can respond behaviorally to the presence of their predators (e.g., Rochette and Dill 2000). Even fisheries science is belatedly recognizing the importance of individual behaviors, especially food–risk trade-offs (cf. Walters 2000).

Fisheries management

Knowledge of the existence of BMIs can contribute to our understanding of the dynamics not only of natural systems, but also of those impacted by human activity, including commercially exploited fishes. Better knowledge of stock dynamics can improve decision making by fisheries managers, as an example will demonstrate. A major recent failure of fisheries management, the largely unforeseen virtual commercial extinction of the Atlantic cod (*Gadus morhua*), has been attributed to a lack of knowledge of indirect behavioral effects. Hutchings (1996) has hypothesized that as the cod stocks declined (and perhaps even more so because of the decline), the remaining fish continued to form large schools, possibly to protect themselves from predators, including harp seals (*Phoca groenlandica*). These schools remained easy to catch despite the stock’s overall decline, so fishermen maintained a high catch per unit effort (CPUE) even as the stock approached commercial extinction, and remained blissfully unaware of the impending crash. It is interesting that although seal predation may have played a role in the cod’s decline, it is quite different from the role that is usually emphasized (i.e., depensatory mortality). Greater awareness of the behavioral responses of the cod to the seals might have prevented an economic and biological disaster.

As discussed earlier, BMIs can facilitate fish capture, but they may also create serious bycatch problems. Tuna such as yellowfin (*Thunnus albacares*) often aggregate with spinner (*Stenella longirostris*) and spotted (*S. attenuata*) dolphins. The reasons for this are not immediately obvious, but for reasons discussed earlier, it is clear that this behavior makes them much easier for tuna fishers to find and catch; nets are simply set

around aggregations, catching tuna but killing many dolphins in the process (Scott 1969, Parrish 1999). The exact nature of the BMII depends on whether dolphins or tuna are the nuclear species in these aggregations. If it is the dolphins (Norris et al. 1985), then a BMII is created between dolphins and fishers (negative for the former and positive for the latter). However, if the tuna are actually the foci for these aggregations (as suggested by Au and Pitman 1986), then the BMII is between tuna and people, facilitated by the aggregation behaviour of the dolphins, and exacerbating the existing interaction between them.

Finally, although it has been recognized that indirect effects are likely to play a major role in determining cascades and other phenomena at the food-web level in marine ecosystems that are important to fisheries (e.g., the Benguela upwelling ecosystem described in Abrams et al. [1996]), the relative importance of DMII and BMII have yet to be investigated.

Conservation

It is critical to understand all of the various and subtle ways that species interact and their dependence upon one another if we are to predict the consequences of changes in community composition due to anthropogenic causes. In Shark Bay, Australia, adult dolphins are seldom eaten by tiger sharks (Heithaus 2001, Simpfendorfer et al. 2001); thus from a purely trophic perspective, the link between sharks and dolphins is a minor one. Yet the behavioral effect of the sharks' presence is dramatic and is likely to cascade throughout the community. Predicting the impacts of global warming on this community (through its effects on shark presence-absence) would probably be impossible without an appreciation of the role of BMII. This is because understanding the species' indirect interactions focuses our attention on the underlying causal mechanisms rather than just the obvious correlations (for example, between water temperature and dolphin distribution).

Finally, it may be worth noting that humans can play any role in a BMII (I, T, or R). We have provided some examples of humans as receivers in earlier sections. But the landscape- (or seascape-) modifying activities of humans make them important "initiators" in many marine systems. For example, causing a prey species to avoid an area as a result of disturbance (from activities as diverse as development or ecotourism; see Frid and Dill [2002]) will cause a local decline in their predators and an increase in their own prey, setting up BMII between humans and all of these other species. The effect may even be exported from the local community. A recent example of this sort has been reported by Lenihan et al. (2001), who showed experimentally that destruction of oyster reefs caused fish to shift their foraging activity to alternative habitats, where they depleted the benthic crustacean populations. Thus, human activity in one habitat can impact populations elsewhere, due to the behavioral decisions of mobile for-

agers. Lenihan et al. (2001) point out that their results have implications for the siting of marine protected areas (MPAs), considering that mobile consumer behavior ensures spatial connectedness with other nearby habitats. Finally, the behaviors of *Homo economicus*, in relation to desirable biotic resources, affect all other components of the ecosystem in which that resource species is embedded, ensuring our species' dubious distinction as the champion "transmitter" of all time (in all systems, not just marine ones). To take a simple example, consider the behavioral decisions around the creation, siting, and stocking of Atlantic salmon (*Salmo salar*) aquaculture facilities, and the potential that these have to affect wild stocks of Pacific salmon (*Oncorhynchus* spp.) in various ways (e.g., Volpe et al. 2001).

There is growing demand for predictive models to guide the development of marine ecosystem policy. Existing models are largely based on quite simplistic assumptions about direct trophic interactions and, less often, density-mediated indirect ones. As these models are developed and tested, we predict that they will commonly fail until a variety of BMII effects are recognized and included. These failures will help to drive considerable productive research on the importance of BMII in marine and other systems.

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