

Marine Conservation Biology

THE SCIENCE OF MAINTAINING THE SEA'S BIODIVERSITY



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10 Multiple Stressors in Marine Systems

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Among the most important challenges facing conservation biology today is the problem of predicting, understanding, and reducing effects of multiple stressors. We define stressors as factors that interfere with the normal functioning of a system (Auerbach 1981); they can either increase or decrease a particular process. Most, if not all, marine systems are exposed to multiple consequences of human activities. Areas near centers of dense population and commerce are often overfished, exposed to repeated introductions of invasive exotics, and serve as the receiving waters for both nutrients and contaminants. More remote areas can also be influenced by larger-scale stressors such as global climate change, ozone depletion, and overfishing of oceanic species, as well as by long-distance consequences of smaller-scale perturbations. As suggested many years ago: “Fortune is not satisfied with inflicting one calamity” (Publius Syrus, 42 B.C.).

In this chapter, we explore how stressors interact in marine ecosystems, and why we should consider stressors in combinations to enhance conservation, management, and restoration efforts. Stressors in marine and estuarine ecosystems have a large number of forms and sources. Most stressors represent the extremes of normal environmental variation that have increased in frequency or severity as a consequence of human activities. In addition, anthropogenic activities can introduce novel challenges, such as synthetic chemicals, to the environment.

Given their ubiquity, several stressors often simultaneously affect organisms, populations, and communities. Nevertheless, both researchers and policy makers typically focus on single issues and concentrate efforts on understanding, and if possible, eliminating or reducing stressors that have strong effects. But studies that focus too narrowly on a single stressor can miss the simultaneous influence of other stressors, thus compromising the utility of results. Similarly, policies that focus on single stressors can also be less successful or cost-effective than actions that take a more holistic approach.

Our goal in this chapter is twofold. First, we will examine the variety of effects of multiple stressors on ecological levels ranging from organisms to whole ecosystems. Second, we will use these examples to emphasize the importance of considering the potential for multiple stressors to shape the structure and dynamics of our marine systems.

Multiple Stressor Effects: Interactive and Noninteractive Effects

Because of both the interdependence of physiological rate processes within individuals and the interdependence of ecological interactions within communities and ecosystems, stressors will almost always interact. Individual stressors fundamentally change the playing field upon which additional stressors act

by selecting for tolerant species and by changing the abundance, distribution, or interactions of structural species (organisms such as kelps and corals that create physical structure upon which other species depend), predators, prey, parasites, and hosts. Such effects can be common when stressors occur simultaneously, but they also occur from exposure to stressors in sequence. For both individuals and ecosystems, the recovery period from a particular stressor can extend beyond the period of exposure, thus influencing their response to subsequent stressors. Effects of stressors on indirect interactions within populations and communities can extend the spatial scale of stressor effects and delay recovery (Peterson et al. 2003), increasing the potential for interactions with additional stressors. On longer time scales, heritable adaptations that increase tolerance to one class of stressors can increase susceptibility to others (e.g., Meyer and Di Giulio 2003).

When multiple stressors affect an individual, population, or ecosystem, the effects can be greater than, less than, or qualitatively different from the sum of the effects that would be predicted if each stressor occurred in isolation. Effects of multiple stressors that are greater than additive, or synergistic, occur because a change caused at the physiological or ecological level by one stressor increases the severity or occurrence of effects of a second stressor. Multiple stressor effects that are less than additive, or antagonistic, can arise because of the extreme severity of one stressor (one stressor might eliminate species susceptible to the second stressor), because the stressors have overlapping effects, or because one stressor reduces the effects of other stressors.

Although weak and indirect interactions are common in food webs (Menge 1995; Paine 1980), total independence is rare. Totally independent physiological effects within an organism are likely to be even less common. Thus, even though ruling out a strictly additive model is statistically difficult, we believe that truly additive, noninteractive multiple stressor effects are rare. Nevertheless, identifying approximately additive stressor effects can be important to management since these are the cases that can be appropri-

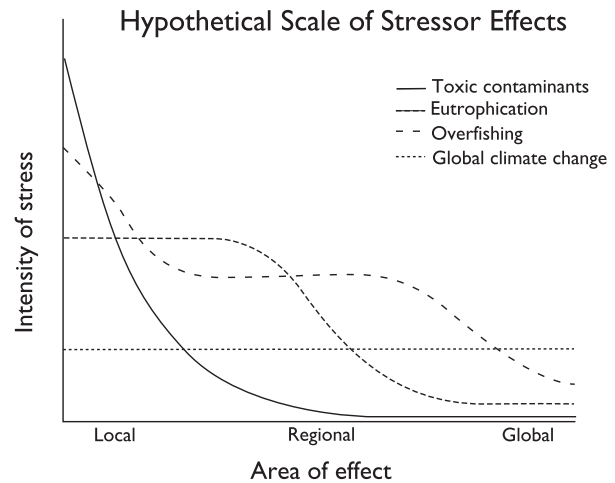


FIGURE 10.1. Different stressors have unique patterns of occurrence and intensity. Some stressors (e.g., chemical toxicity from pollution) are very intense on a local scale but relatively weak on a wide scale, while others (e.g., global climate change) can be widely distributed. As a consequence, the importance of stressor interactions can depend on the scale of the system being addressed. The relative importance of stressors will vary among sites when viewed on a local scale.

ately studied and managed by focusing on individual stressors.

The strength and importance of stressor interactions also vary with spatial scale and location. Although the presence of stressors is nearly ubiquitous, the scale at which specific stressors act plays an important role in how they interact. Some stressors are very intense locally, especially in coastal areas near dense population centers, but act over a very short range, while other stressors tend to be weaker locally but are nearly global in extent (Figure 10.1).

In the following sections, we describe several potentially important kinds of multiple stressor interactions. Our goal is not to provide an exhaustive review of each topic, but instead to provide an indication both of the wide range of stressors whose interactions might be important to marine organisms and ecosystems, and of the wide range of mechanisms by which potentially important stressor interactions occur.

Examples of Interactions among Stressors in Marine Systems

Nutrient Loading and Overfishing

Reductions in fished species and increased nutrients are two of the major consequences of human activities in marine systems (see Chapter 7 and Chapter 11 through Chapter 15), and frequently co-occur in coastal and enclosed waters (Caddy 2000; Cloern 2001; Jackson et al. 2001). Each has the potential to alter productivity, diversity, biomass, and the extent and suitability of critical habitat. Depending on the part of the food web most strongly depleted by fishing pressure, fishing and nutrient loading can act synergistically or antagonistically. Synergistic effects between overfishing and other stressors can cause sudden shifts in abundances and community composition as functional redundancy and spatial refuges are eliminated (Jackson et al. 2001).

Where overfishing reduces populations of herbivores or suspension feeders that consume primary producers, it also potentially increases the deleterious effects of anthropogenic nutrient loading. This occurs because both increased nutrients and reduced consumption can result in increased standing stocks and altered species composition of primary producers. The decline of the Eastern oyster (*Crassostrea virginica*) due to overfishing and disease has reduced top-down control of phytoplankton in the Chesapeake Bay (USA), increasing the amount of unconsumed phytoplankton carbon available to microbial decomposition that depletes dissolved oxygen, and potentially increasing the magnitude of nutrient reduction that will be required to improve water quality (Newell and Ott 1999).

Removal of apex predators through fisheries potentially leads to the same results as direct removal of herbivores. In lakes, reduction or elimination of piscivores can increase populations of zooplanktivorous fishes, decrease populations of zooplankton, and thus decrease top-down control of phytoplankton (Carpenter and Kitchell 1993; Hairston et al. 1960). Polis and Strong (1996) argue that the prevalence of omnivory and the complexity of marine food webs make the effects of changes in consumption by apex predators dif-

ficult to predict in marine systems. However, at least some marine systems exhibit classic lake-like trophic cascades. Overfishing of piscivores in the Black Sea has reduced top-down control on phytoplankton and allowed primary producers to respond more strongly to anthropogenic nutrient enrichment (Daskalov 2002). The potential for interactive effects of fishery removals and nutrients clearly indicates the importance of coordinated management of fisheries and nutrient loading; fishing pressure potentially increases both the cost and technological difficulty of correcting nutrient overenrichment in coastal waters. As problematic, the reliance on fishery yields supported by overenrichment of coastal ecosystems can increase the political difficulty of reducing nutrient loading.

In theory, fishing practices that decrease abundances of zooplanktivorous fishes, or reduce predation pressure on herbivores, should increase the flow of material from primary to secondary producers, and at least partially counteract the deleterious effects of increased nutrient loading. Manipulations of fish populations to reduce algal and macrophyte standing stocks are, in fact, used as management strategies in relatively closed freshwater systems (Hansson et al. 1998). Newell and Ott (1999) have suggested floating rack aquaculture of bivalves as a means of removing excess production from eutrophic marine systems. The potential for bivalve aquaculture to exceed the carrying capacity in coastal embayments is an economic and ecological concern. With the exception of bivalve aquaculture, however, fishery-induced changes in marine food webs that exacerbate nutrient loading consequences appear to be more common; we know of no other examples of fishery-induced changes in marine food webs that have reduced the effects of anthropogenic nutrient loading.

High nutrient loadings and fisheries can also interact in ways that alter fisheries' yields and increase the potential for fisheries to deplete targeted populations. In addition, a single type of initial stressor, in this case, high nutrient loading, can have multiple cascading effects creating additional, sometimes interacting stresses on fished species and the ecosystems in which they occur. Caddy (1993) has suggested that, together, nu-

trient enrichment and heavy fishing pressure lead to alterations in food webs such that fishery production increases initially in formerly oligotrophic systems, but then experiences negative changes as systems become more eutrophic. Global comparisons across marine systems, and over time within systems, indicate a positive relationship between fishery landings and nitrogen loading (Nixon 1992; Nixon and Buckley 2002). But high nutrient loadings can lead to low fish abundances in areas with reduced dissolved oxygen (Breitburg 2002; Rabalais, Chapter 7), as well as the loss of submersed macrophytes, which can, in turn, lead to reduced populations of both fish and their prey. Trawling surveys show reduced abundance and diversity of finfish during periods of low dissolved oxygen, probably reflecting both avoidance of unsuitable habitat and mortality (Baden and Pihl 1996; Breitburg et al. 2001; Craig et al. 2001; Eby et al. 1998; Howell and Simpson 1994). Hypoxia and anoxia can also lead to extensive mortality of fish eggs (Breitburg 1992; Breitburg et al. 2003; Nissling et al. 1994) and sessile invertebrates (Rosenberg 1985) that lack the capacity for behavioral avoidance of oxygen-depleted waters. In addition, by affecting behavior, hypoxia can make some species more susceptible to fishing, ultimately leading to decreased stock densities. For example, in the Kattegat, Norway lobsters (*Nephrops norvegicus*) are more available to the fishery during periods of low dissolved oxygen because they tend to emerge from their burrows (Rosenberg 1985), and catches of demersal fishes increase as fish migrate out of hypoxic waters (Kruse and Rasmussen 1995). Because of changes in abundance and behavior, fish and shellfish populations in parts of systems experiencing nutrient-induced hypoxia may support lower catches and be more susceptible to overfishing.

Interactions of Trace Elements with Nutrients and Other Trace Elements in Controlling Primary Production in Marine Environments

Trace elements enter marine systems through a variety of routes, ranging from localized point sources to global atmospheric contamination. Interactions

among trace elements, and between trace elements and nutrients, provide examples in which the abundance and distribution of one stressor can affect the expression and severity of another stressor (Figure 10.2). Trace elements can act either as micronutrients or as toxic elements, and many, for example copper, selenium, and zinc, can act in either role, depending on concentrations or ratios to other elements. The physiological effects of both toxic and necessary trace elements are often closely tied to nutrients because trace elements often act as chemical analogues for nutrients and as cofactors in enzymes that transport or assimilate nutrients. Experiments designed to set regulatory limits that do not consider such multiple stressor interactions can significantly overestimate the ability of populations to tolerate contaminants under ambient nutrient and trace element concentrations.

How the effects of trace elements, both beneficial and harmful, interact with those of other trace elements and nutrients is not completely clear. Each element and nutrient has its own unique pattern of cycling and distribution. Differences in these patterns produce regions in the marine realm where particular elements or nutrients can be either limiting or potentially toxic to particular groups of primary producers, and where other interacting elements can either promote or relieve those limitations or toxicities.

Many anionic trace elements act as analogues of chemically similar nutrients (Riedel 1985; Riedel and Sanders 1996). For example, arsenic is chemically similar to phosphorus and appears to be transported into phytoplankton by the phosphate transport system, decoupling phosphorylation and resulting in less efficient energy metabolism. Algae appear to have adapted to the problem of arsenic and phosphorus interactions by developing mechanisms for transforming and excreting it from cells as dimethylarsenic (DMA) (Sanders and Riedel 1993; Sanders and Windom 1980). Seasonal patterns in DMA versus arsenate concentrations in the estuarine Patuxent River (a sub-estuary of Chesapeake Bay, USA) indicate that phytoplankton are responding to arsenic stress during peri-

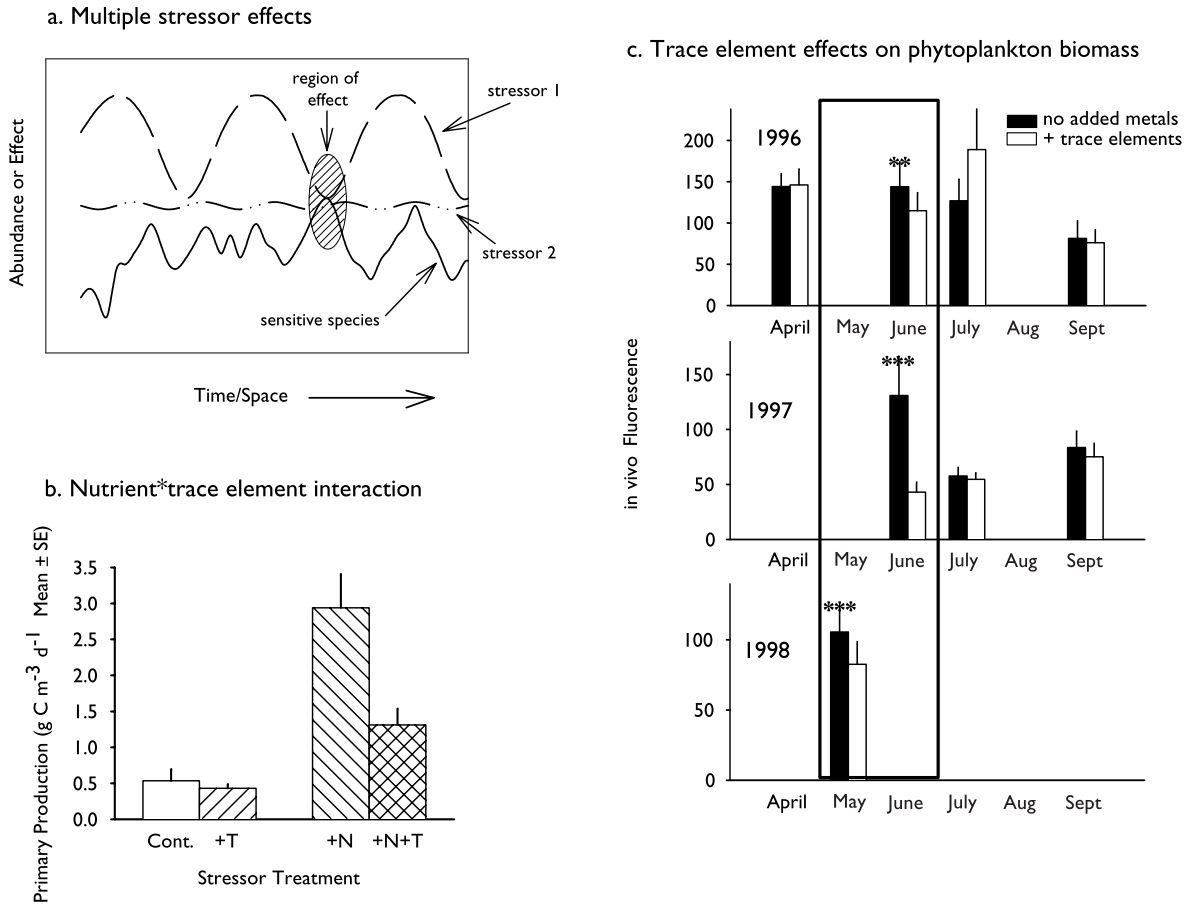


FIGURE 10.2. Spatial and temporal patterns of stressor interactions, as well as the presence and importance of sensitive species can determine when and where multiple stressor interactions strongly influence individual species as well as system-level processes. 10.2a: The region of effects of multiple stressor interactions in time and space can be determined by patterns of variation in each individual stressor and susceptible species. 10.2b: When and where multiple stressor interactions occur, stressor interactions can reduce the effects of individual stressors. In this example (from Breitburg et al. 1999), the level of phytoplankton primary production in estuarine mesocosm experiments was similar in control tanks (Cont.) and tanks to which only trace elements (Cu, As, Cd, Ni, and Zn; +T) were added. However, the addition of the same concentration of trace elements in tanks to which nutrients were also added (+N+T) greatly reduced phytoplankton response to nutrient additions (+N). 10.2c: The trace element by nutrient interaction depicted in Figure 10.2b shows a regular seasonal pattern that is most likely controlled by background seasonal patterns of phosphate concentrations and limitation, arsenate:phosphate ratios, and the complexing capacity of estuarine waters.

ods of phosphorus limitation but not during periods of nitrogen limitation (Riedel 1993; Riedel et al. 2000).

Mesocosm experiments in the Patuxent River estuary also indicate a strong seasonal pattern of trace element toxicity related to nutrient and trace element

interactions (Breitburg et al. 1999; Riedel et al. 2003; Figure 10.2). Additions of low levels of trace elements (arsenic, cadmium, copper, nickel, and zinc) substantially decreased phytoplankton and bacterioplankton responses to increased nutrient loadings only in

spring, when phosphate concentrations were low, nitrogen to phosphorus ratios were high, and species sensitive to arsenate were abundant (suggesting nutrient and arsenic interactions). However, these additions had no detectable effect during summer. Experiments in spring in which metals were added separately indicated that both arsenic and copper were toxic at low nutrient loadings, while only copper was toxic at high nutrient loadings (Riedel et al. 2003). These experiments indicate that interactions between nutrients and trace elements can alter patterns of spatial and temporal variability within marine systems. In addition, because trace elements have the potential to mask or reduce the effects of high nutrient loadings, making precise predictions of the benefits of nutrient reduction strategies will be more difficult where trace elements are elevated along with nutrients.

An interesting and highly controversial proposal would use an important trace element and nutrient interaction to ameliorate effects of anthropogenic carbon dioxide production and consequent global warming. Iron is a required micronutrient that acts as a catalyst in nitrate reduction and assimilation (Rueter and Ades 1987). Iron is relatively insoluble in seawater and present in very low concentrations. In several large areas of the ocean with high nutrient availability but low chlorophyll (HNLC; Frost 1991), iron apparently limits primary productivity (DiTullio et al. 1993). Relieving iron limitation in HNLC areas could theoretically increase primary production and remove additional carbon dioxide from the water, thus increasing the flux of carbon dioxide from the atmosphere (Martin and Fitzwater 1988). Global models of marine ecosystems suggest that primary production, community structure, and carbon sequestration are all dependant on atmospheric iron inputs, particularly in HNLC regions (Moore et al. 2002). However, field experiments to date have yielded mixed results and further illustrate the complexity of addressing large-scale multiple stressor interactions; factors other than iron itself will also determine whether fixed carbon remains in the surface layer or is sequestered in the deep ocean (Boyd et al. 2000).

Interactions of Disease and Parasites with Other Stressors

Microbial pathogens and multicellular parasites are ubiquitous components of natural ecosystems. But increased intensity and prevalence of microbial diseases and parasite infections are common in coastal systems with high levels of chemical and sewage contamination (e.g., Kennish 1997). In addition, disease or parasitic infection can lower the resistance of organisms to other stressors (e.g., Brown and Pascoe 1989).

Suppression of immune system responses resulting from exposure to physical, physiological, or contaminant stress has been demonstrated experimentally in both invertebrates and fish, and is supported by evidence from field-collected animals. For example, juvenile chinook salmon (*Oncorhynchus tshawytscha*) collected from an urban estuary or exposed to sublethal doses of polyaromatic hydrocarbons (PAHs) and polychlorinated biphenyls (PCBs) in the laboratory showed suppressed leukocyte production of plaque-forming cells (Arkoosh et al. 1998a and 1998b). Similarly, mussels collected from contaminated sites or experimentally exposed to copper showed reduced immunocompetence compared with mussels collected from cleaner sites (Dyrynda et al. 1998; Pipe et al. 1999).

This decreased immune response can lead to detectably increased disease occurrence and severity. Juvenile chinook salmon from the urban estuary described above were more susceptible to mortality from the bacterium *Vibrio anguillarum* than were salmon from the nonurban estuary or hatcheries (Arkoosh et al. 1998a). Eastern oysters exposed to tributyl tin (TBT) at concentrations within the range observed in marinas and harbors where TBT was used (Anderson et al. 1995; Fisher et al. 1999), and those exposed to the water-soluble fraction derived from contaminated sediment from the Elizabeth River, Virginia, USA (Chu 1996), showed increased rates of infection and mortality from Dermo (caused by the protist *Perkinsus marinus*; Mackin et al. 1950).

In addition to compromising immune responses,

contaminant exposure can sometimes break down the natural physical barriers to infection. Fish gills are a relatively susceptible site. A wide variety of chemical contaminants and physiological stresses have been shown to increase the occurrence of gill ciliates (Lafferty and Kuris 1999), which decrease the efficiency of oxygen transfer and make fish more susceptible to pathogens.

Under some circumstances, contaminants or natural stressors can also decrease disease or parasite prevalence, or the severity of their effects on host organisms; that is, the effects of multiple stressors can be less than additive. Stressors can decrease parasites by reducing host population size, causing direct mortality or physiological stress to the parasites, altering habitat, or otherwise reducing the efficiency of transmission (Lafferty and Holt 2003; Lafferty and Kuris 1999). The complex life cycles of many parasites can make them highly susceptible to stressors because completion of their life cycle can be negatively influenced by stressor effects on any one of a series of host species and habitats. In addition, the susceptibility of many parasites to stressors is illustrated by the use of copper, formalin, and toxic organic dyes (compounds that ordinarily would be considered contaminants themselves) for treatment of fish diseases.

Parasites can also be more susceptible to natural stressors than are their hosts. Two diseases, MSX (caused by *Haplosporidium nelsoni*; Andrews 1966) and Dermo, have seriously impacted populations of the Eastern oyster throughout much of its natural range. Both MSX and Dermo are less tolerant of low salinity than is the oyster (Ford and Tripp 1996; Mackin 1956). Temperature is also a costressor in oyster disease. Mortality caused by both Dermo and MSX occurs during the hottest season of the year (Andrews 1965). The warm, dry, higher-salinity conditions associated with La Niña events and long-term trend of increasing winter temperatures along the Atlantic Coast of the United States during the past 25 years might have caused the apparent increase in disease incidence on the East and Gulf coasts (Harvell et al. 1999; Kim et al., Chapter 9).

Disease and other stressors such as overfishing and physical disturbance can also interact in an ecological context, rather than within individuals. For example, overfishing of finfish on Caribbean coral reefs greatly reduced herbivory by fish species that feed on benthic macroalgae, which potentially outcompete coral recruits (Hay 1984; Hughes 1994). With the decline in herbivory by fish and reduced predation on sea urchins by fish, sea urchins became relatively more important as grazers of macroalgae. Coral abundance and diversity persisted until the occurrence of the sea urchin disease that greatly reduced densities of the dominant sea urchin *Diadema antillarum* over large areas of the Caribbean (Lessios 1988). As sea urchin densities declined and macroalgae increased and outcompeted coral recruits, the abundance of live corals dramatically declined and reduced reefs' ability to recover from hurricane damage (reviewed in Hughes 1994). The combined effects of overfishing and disease were greater than that of either alone because, together, they reduced the total community herbivory and eliminated the potential for compensatory responses by one set of herbivores as the other declined. This reduction in total herbivory then made the community more susceptible to a third stressor: physical disturbance due to storms.

Are Stressed Systems More Susceptible to Invasions?

If the effects of an initial stressor can make an individual more susceptible to subsequent stressors, is the same true for communities and ecosystems? In 1958, Elton noted that "the brunt of these invasions [of nonindigenous species] has been borne by the communities much changed and simplified by man." Disturbed systems may be more susceptible to invasions than are systems retaining their full diversity and density of native species. Recent experimental evidence supports the idea that low diversity increases susceptibility of benthic marine communities to invasions (Stachowicz et al. 1999, 2002a). Human activities including climate change, increased nitrogen

deposition, altered disturbance regimes, and increased habitat fragmentation, as well as overfishing have been suggested to increase the prevalence of invasive nonnative species (Carlton 1992; Dukes and Mooney 1999; Stachowicz et al. 2002b).

Overfishing can make a system more susceptible to invasions by reducing the abundance or diversity of native species that are potential predators and competitors, and by indirectly altering prey abundance. Similarly, eutrophication can increase the abundance or alter the composition of prey, by either directly (e.g., through oxygen depletion) or indirectly (e.g., through food web interactions) altering predator and prey populations. For example, factors such as depletion of mackerel (*Scomber scombrus*) through overfishing, freshwater diversions that altered distributions of mackerel and other fishes, and eutrophication that altered and increased prey abundance are all thought to have favored gelatinous zooplankton in the Black Sea (Caddy 1993; Shiganova 1998; Zaitsev 1992), thus leading to a dramatic increase in the abundance of native *Aurelia* jellyfish from 1972 to 1992. Conditions favoring gelatinous zooplankton likely enhanced the invasion by the ctenophore *Mnemiopsis leidyi*, which was introduced into the Black Sea in ballast water in the 1980s (Shiganova 1998). *M. leidyi* abundance increased dramatically in the years following its introduction and is thought to have contributed to the collapse of additional fish stocks during the late 1980s and early 1990s via competition and predation (Kideys 2002; Shiganova 1998).

Besides being more susceptible to invasions, areas where the habitat is highly altered by human activities (e.g., agricultural systems, urban areas, seaports) also tend to be the locales with the highest rates of introduction of nonnative species. Exchange of ballast water in seaports has been a major source of marine introductions (Carlton and Geller 1993; Ruiz et al. 2000; Carlton and Ruiz, Chapter 8), including algae and dinoflagellates associated with harmful blooms and toxin production (Macdonald and Davidson 1998). The San Francisco Bay area now harbors at least 234 exotic species and another 125 species that can-

not be identified clearly as native or exotic (Cohen and Carlton 1998). Human alteration of the system is thought to have contributed to the success of the invasions (Carlton 1979).

In marine systems, as elsewhere, human alterations also influence the rate and pattern of *intentional* introductions. Depletion of native stocks of fished species has led to the introduction of exotic species to bolster commercial, artisanal, and recreational fisheries. For example, the depletion of the native European flat oyster (*Ostrea edulis*) was an impetus for the importation and introduction of the Eastern oyster to England during the late 19th century (Carlton and Mann 1996), and decimation of the native Eastern oyster in Chesapeake Bay by a combination of overfishing and disease (including an introduced pathogen) has led to a proposal by Maryland and Virginia to introduce the Suminoe oyster (*Crassostrea ariakensis*; NRC 2003). Nonnative species have also been introduced in attempts to restore damaged habitat. For example, smooth cordgrass (*Spartina alterniflora*), a problematic invasive along the Pacific Coast of the United States, was introduced into San Francisco Bay in the 1970s for marsh restoration (Callaway and Josselyn 1992).

When Everything Goes Wrong: The Eastern Oyster in Chesapeake Bay

“O, Oysters come and walk with us!,”
The Walrus did beseech. . . .
. . . . But answer came there none—
And this was scarcely odd, because
They’d eaten every one.

(Lewis Carroll, *The Walrus and the Carpenter*,
Through the Looking Glass, 1871)

We have cited problems of the Eastern oyster in the Chesapeake Bay in the preceding sections because it serves as an example in which many stressors acted over long periods of time to devastate a fishery important to the economics and culture of a region (Figure 10.3). A more thorough consideration of the plight of the Eastern oyster in the Chesapeake Bay il-

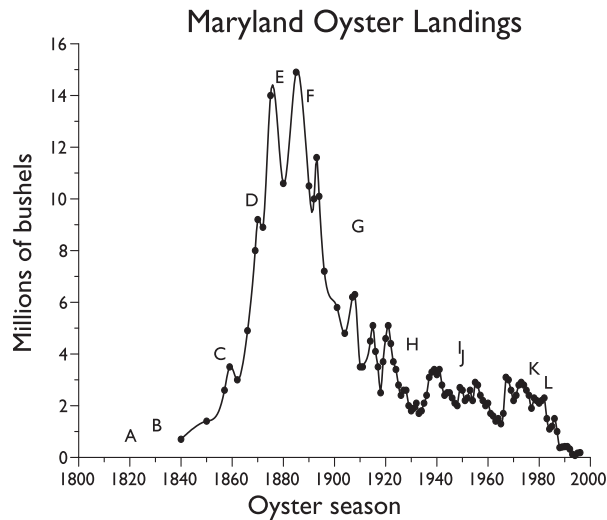


FIGURE 10.3. A history of the oyster fishery in Chesapeake Bay in Maryland. (A) 1820, first Maryland oyster law, dredging prohibited; (B) 1830, first law establishing legal oyster aquaculture; (C) 1854, dredging legalized; (D) 1868, Maryland Oyster Police established; (E) 1878–79, Winslow Report, first scientific study of oyster beds in Maryland; (F) 1890, Cull Law, sets size limit (2.5 in.) and mandates return of shell; (G) 1906, Yates Survey of oyster bars; (H) 1927, size limit raised to 3 in.; (I) 1949, Dermo reported in Chesapeake Bay; (J) 1951, state begins shell planting programs; (K) 1983, MSX epidemic kills 50 percent of oysters in Nanticoke River, Maryland (Heeden 1986); (L) 1985–1987, major epidemic of Dermo (Burreson and Calvo 1996). Historical oyster harvest data from Kennedy and Breisch (1981), recent data from National Marine Fisheries Service (courtesy of George Abbe).

illustrates the complexity of considering and managing the myriad of anthropogenic stressors that affect coastal systems. The list of stressors on the Chesapeake Bay oyster population includes habitat changes, over-fishing, pollution, and disease.

At the time of the arrival of European settlers, the Chesapeake Bay was vastly different from today. Extensive forests were effective at retaining and transpiring rainfall, so that runoff was less than it is now and more evenly distributed seasonally. In addition, the forests were efficient sinks for airborne nutrients, which were in much lower supply (Boynton et al.

1995). Consequently, much of the Chesapeake Bay had higher salinity, lower density gradients, and lower primary productivity. Because forests had not yet been turned into cropland, the Chesapeake Bay suffered from less erosion and suspended particles and benefited from greater water clarity and light penetration (Schubel 1986). As a result, the Bay and many of its tributaries hosted extensive oyster reefs.

With the cutting of the forests, conditions began to change. Pollen analysis shows evidence of extensive clearing by 1760, with 80 percent deforestation by the mid-19th century (Brush 1989; Cooper 1993). Phytoplankton communities in the Chesapeake Bay changed after 1800, with greater proportions of planktonic brackish water- and nutrient-tolerant species, and lower proportions of oligotrophic marine diatoms (Cooper 1993). Increased runoff reduced the salinity in the upper portions of the Bay and its tributaries. In addition, greater sedimentation from increased erosion (Cooper 1993) buried many oyster beds in mud and restricted the habitat (Mackenzie 1996).

The increased runoff and salinity stratification also enlarged the area and duration of seasonal anoxia in the bottom waters of the Bay, which further decreased the habitat for oysters and produced kills of oysters even in shallow water (Officer et al. 1984; Seliger et al. 1985). The first signs of serious anoxia problems in the Bay occurred in the sediment coincident with the early period of European settlement (Cooper 1993; Cooper and Brush 1991).

During the 19th century, the oyster fishery became a significant factor for the oyster population as fisherman depleted stocks in New England and moved southward (Heeden 1986). Extensive damage to the physical structure of oyster reefs was caused by the tonging and dredging of oysters, and the fact that little of the shell (the prime site of oyster settlement) was returned to the Bay. Reef destruction can also increase the susceptibility of oysters to hypoxia and anoxia by reducing the percent of oyster biomass that extends into the oxygenated layer of the water column (Lenihan and Peterson 1998). Nevertheless, Chesapeake oyster landings throughout much of the 19th century

remained astonishingly high compared with current landings (see Figure 10.3).

Increasing population and industrialization also led to problems with contaminants. The port towns of Baltimore and Norfolk grew to be major hot spots for contamination (Helz and Huggett 1987; Sinex and Helz 1982). By the early 20th century, some contaminants were elevated substantially baywide above presettlement concentrations (Goldberg et al. 1978; Owens and Cornwell 1995). Electrical generating stations built with copper and nickel alloy condensers in the 1950s and '60s had oyster populations nearby with extremely high trace element concentrations. Oysters with green meat from copper accumulation had a bitter taste and could cause sickness if eaten in large amounts (Abbe 1982; Loosanoff 1965).

Undoubtedly, nutrient loadings have increased dramatically in Chesapeake Bay (Cornwell et al. 1996) and become a major management problem (Kemp et al. 1983). Until recently, on a historical scale, crop fertilization used natural fertilizers generated by local livestock that were fed local crops or other translocations of biomass (e.g., fish). The floodgates to eutrophication opened worldwide when a method to produce ammonia fertilizer from nitrogen and hydrogen gases was commercialized in the 1930s. Soon, crops were extensively fertilized with nitrogen and phosphorus, much of which was destined to run off into local water bodies. High nutrient loadings further contribute to the problem of seasonal oxygen depletion, alter the phytoplankton community in undesirable ways, encourage predators that feed on larval oysters (e.g., ctenophores), and encourage the growth of epifauna and disease organisms.

Disease has been a major factor in the oyster fishery for much of the 20th century. Some preserved samples from the 1930s show evidence of Dermo, but the disease likely occurred earlier (personal communication with Gene Burreson, Virginia Institute of Marine Sciences, Gloucester Point, Virginia, USA). MSX was imported from elsewhere in conjunction with transplants of nonnative oysters (Burreson et al. 2000). The increased prevalence and intensity of the

diseases in Maryland waters in the 1980s was likely encouraged by a three-year drought (and consequent high salinities), as well as movement of shell and juvenile oysters in programs to ameliorate stock depletion from overfishing (Burreson and Calvo 1996).

In summary, the question regarding oysters in the Chesapeake Bay is not so much what is wrong, but rather what is left that is right. The large number of interacting stressors on the oyster population has made efforts to understand and reverse the oyster population declines difficult. Fishing pressure certainly has been an important cause of oyster mortality. However, regulating the fishery alone is not likely to be sufficient. Our understanding of direct toxicity of pollutants to oysters does not suggest widespread problems from toxicity. Why the diseases have become so much more prominent is not evident, although eutrophication and climatic change may be factors. Has the oysters' disease resistance been lowered by chronic toxic stress and hypoxia, or by changes in the habitat due to eutrophication, high sediment loads, and loss of reef structure? Much of what is wrong is probably due to large-scale problems, which will yield only to massive and disruptive changes in our current land use patterns and fishing practices, along with extensive habitat restoration. Correcting only a single stressor is unlikely to lead to successful restoration of oysters to Chesapeake Bay.

Conclusions

Stressors occur in a virtually infinite number of possible combinations and affect systems ranging from single cells to entire communities and ecosystems. The examples of multiple stressor interactions we have selected have been chosen to demonstrate the ubiquity and importance of multiple stressors, as well as the wide variety of phenomena, from physiology to community ecology, that give rise to interactions among stressors in marine systems

Most of the multiple stressor interactions we have discussed are detectable at small spatial scales in near-shore ecosystems or semi-enclosed water bodies. But

larger-scale, longer-duration interactions might be as important, or more important, than local processes. Human-influenced alterations in the landscape will interact with stressors that influence local spatial and temporal patterns of larval supply to alter recruitment success of marine plants and animals. The probability that assemblages will recover from a large-scale natural disturbance may depend on how human activities have affected species' abundances and ecological interactions on both local and larger spatial scales. Time lags can be especially important when considering stressor interactions. As the example of the loss of herbivores on Caribbean reefs illustrates, the full consequences of an initial stressor might not be completely expressed until subsequent stressors challenge the system. Finally, all other human influences will be overlain by, and potentially interact with, the effects of global climate change. Changes in temperature regimes and precipitation will alter biological distributions, physiological, and geochemical rate process, and the ways that these interact with other natural and anthropogenic stressors. Changes in environmental variability caused by both natural and human-influenced processes will likely affect the relative success of various life history strategies, as well as mechanisms that influence the probability of species coexistence.

The frequency with which we discussed "potential" or "likely" outcomes of multiple stressor interactions in this chapter is a reflection of how poorly the importance and magnitude of stressor interactions are understood. Because urbanized or otherwise contaminated systems contain a multitude of potential stressors, the exact interactions between particular chemicals or nutrients and disease agents are often difficult to determine. Experiments to determine the nature of stressor interactions must carefully incorporate temporal and spatial patterns of both stressors and biotic variability. But such controlled experiments can rarely be used to assess the importance of stressor interactions at large spatial and temporal scales. Whole-system manipulations have resulted in tremendous gains in our understanding of closed freshwater systems. Researcher-initiated whole-system manipulations will

be more difficult in large or open systems and have limited opportunity for numbers of treatment combinations or levels. However, strategic examination of whole-system or large-scale manipulations created by management action or inaction is an invaluable tool that can be used to improve the understanding of multiple stressor interactions. Investment in long-term monitoring and close collaboration between empiricists and modelers will be critical to the success of this approach.

In spite of the inherent difficulties, it is important for successful natural resource management and conservation that managers, researchers, and policy makers consider the myriad of stressors to which natural systems are exposed. Multiple stressor interactions not only alter the magnitude of stressor effects but also alter the patterns of variability and predictability on which management strategies often rely (Breitburg et al. 1998, 1999). Multidisciplinary research approaches are required for such efforts to seriously address the magnitude and consequences of multiple stressor effects. In addition, the current model in which separate government agencies are typically responsible for water quality and resource management should be reexamined. Such division of authority and focus potentially hinders efforts to restore and prevent further damage to systems in which both the habitat and the organisms, themselves, are affected by human activities. Directly addressing the complexity of multiple human influences on natural systems, along with the complexity of the systems themselves, will provide the greatest chance for successful conservation and management efforts.

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