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AS I SEE IT

Marine species invasions in estuaries and harbors

John C. Briggs*

Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97333, USA
Present address: 43939 Spiaggia Place, Indio, California 92203, USA

ABSTRACT: The biodiversity of most marine communities is more or less dependent on continuous invasions from sources with greater richness. These ongoing, natural invasions have become greatly augmented by ship traffic in numerous estuaries and harbors where the native biota has been diminished or lost due to habitat destruction and pollution. Some of the invaders proved to be pests, indicating that these kinds of human introductions need to be controlled, but the ultimate management problem is that the invaders have generally increased diversity at the lower trophic levels after the top-level predators were lost or diminished. During the past 20 yr, work on habitat improvement has been progressing within many estuaries. But so far there is little evidence of the final step in restoration, which should be the revival of a balanced, more productive ecosystem. The inflow of invasions can be lessened by the prevention of ballast water release, pollution control, and habitat improvement. These changes should be followed by steps to reintroduce apex-level predators in order to restore natural ecosystems.

KEY WORDS: Marine invasions · Human introductions · Biodiversity · Trophic levels · Transplantation · Conservation

INTRODUCTION

With regard to species that migrate or are introduced from one locality to another, there has been and still is an unfortunate disconnect between biogeography and ecology. For many years biogeographers have recognized the existence of continuous invasions or migrations among the world's regions and provinces (Briggs 1974). More recently, marine ecologists have been interested in examining the contemporary effects of invasive species at the community level (Ricklefs 1987, Karlson et al. 2004, Witman et al. 2004). The biogeographic and ecological studies agree in 3 respects: (1) there is a continuous movement of species among areas and communities; (2) such movements almost always involve migrations from locations that are relatively species rich to those that are relatively poor; and (3) species that colonize new communities are generally accommodated by the native species that occupy the appropriate habitats. The term 'accommodation' refers to a proposed rule, which states that if an exotic species colonizes a native ecosystem it is permitted to do so by an accommodation on the part of the native species that occupies appropriate habitat (Briggs 2010). Accommodation means the yield of living space or the provision of support to the invader as the result of competitive pressure, including special relationships described as niche compression, niche sharing, facilitation, or mutualism. When such special relationships are not identified, it would seem prudent to use accommodation as an inclusive term. The ultimate goal of restoration ecology should be the introduction or reintroduction of large-size, apex-level predators. Despite the numerous ongoing restoration projects, there are no indications of improvements to the extent that this goal can be realized.

ESTUARIES, HARBORS, AND BAYS

In coastal locations such as estuaries, harbors, and bays, where the natural pace of invasions has been

*Email: clingfishes@yahoo.com

greatly augmented by human introductions via ship traffic, it has been difficult to obtain a balanced perspective on the effects of invasions. Individual invader species are usually investigated because they have had an economic impact (Ruiz et al. 1997), i.e. they are considered pests due to their adverse effects on local structures (piers, seawalls, intake pipes) or they interfere with human activities such as fishing, boating, and aquaculture. Consequently, much of the scientific literature dealing with coastal invasions is devoted to such pest species. As a result, the local discovery of an exotic species is often accompanied by expressions of alarm and speculation that native species will be harmed or driven to extinction (Jousson et al. 2000). This kind of publicity, produced by the media and some scientists, gives the impression that areas with ship traffic are under continuous bombardment by a host of harmful species. Some conservation organizations have undertaken the task of detecting any invaders in order to eliminate them before they become established (Delaney et al. 2008).

From a global viewpoint, it appears that invasions into disturbed habitats are more common in temperate than tropical waters. Localities such as San Francisco Bay, Chesapeake Bay, Tokyo Bay, and some of the southern Australian harbors demonstrate relatively high numbers compared to lower latitude destinations in Australia, Asia, and Africa (Hutchings et al. 2003, Briggs 2010). These observations are consistent with fossil data that indicate a higher rate of extinction in temperate zones, thus providing more room for invaders (Krug et al. 2009). The higher native biodiversity in the tropics, despite some reduction in disturbed areas, may be more effective in preventing invasions. Exceptions are found at tropical harbors located at isolated islands such as Hawaii and Bermuda where native diversity is limited.

The current emphasis on the destructive effects of a relatively few exotic species has resulted in many erroneous statements. Some ecologists have called invasive species a 'threat' to marine biodiversity. Observations of this kind influenced the World Conservation Union (IUCN 2003) to rate invasive species as one of the 4 greatest threats to the world's oceans, and to publish a set of guidelines for the prevention of biodiversity loss caused by alien invasive species. It has been observed that some invaders may cause an ecological 'meltdown' by transforming initially benign introductions into aggressively expanding invasions (Simberloff & Von Holle 1999, Grosholz 2005). Molnar et al. (2008, p. 485), in their article on the global threat of invasive species, stated: 'Invasive species are widely recognized as a major threat to marine biodiversity.'

Why are the foregoing statements erroneous? In terms of common use, and especially with respect to conservation implications, biodiversity is equivalent to species richness. Under this definition, there is no way that an invader can cause a biodiversity loss unless its establishment results in the extirpation of more than one native species (in using this definition, I do not imply that biodiversity cannot be measured using other criteria). Although there are several hundred recorded invasions by exotic species into coastal and large estuarine localities in various parts of the world, there have been no complete (global) extinctions among the native species as a result of the invasions (Briggs 2007). The term 'meltdown' is misleading, as it gives the impression of an ecological catastrophe or calamity whereas it actually means a beneficial or facilitative interaction between invader species. Even when such interaction has resulted in a rapid expansion of invader species, there are no indications that native species were completely extirpated from their original ranges (Briggs 2010). Invasive species cannot be a threat to marine biodiversity because their presence almost always results in a species diversity increase, not a decrease.

Considering the evidence that invader species do not cause losses of species diversity, how do such losses occur? Local marine species diversity is reduced when habitats are eliminated by a variety of human activities. Many natural bays and estuaries have been physically altered by dredging and by seawall, bridge, and other construction. Because such areas tend to have concentrated human populations, they are also likely to be impacted by increased pollution (organic and inorganic) and overfishing. Once the native populations have been reduced by these changes, resistance to invasion is reduced as well, and the areas become invaded by organisms that can tolerate the physical environment (Reise et al. 2006). This cause and effect has been documented to occur on a global scale (Byrnes et al. 2007). In harbors, many such organisms are introduced via ship traffic and thrive due to the increased nutrients. In these highly invaded areas, it is human activities, not the invaders, that have caused the depletion of native species (Lotze et al. 2006). In fact, invaders, even though some of them may be pest species, are usually responsible for increases rather than decreases in biodiversity. There is an increasing realization that some non-native species are beneficial and have conservation value (Schlaepfer et al. 2011).

Is increased biodiversity in and of itself an advantageous effect of invasions? Comparison of records from coastal ecosystems has shown that those with higher species richness demonstrated lower rates of collapse of commercially important fish and invertebrate taxa over time (Worm et al. 2006). This information is consistent with the current consensus among ecologists about the value of biodiversity to ecosystem function (Hooper et al. 2005). For many years, a primary goal of conservation societies has been to prevent the further loss of biodiversity, particularly within local areas where diversity has been impacted by human activities. On the other hand, there has been relatively little interest in the enhancement of biodiversity, at least in the marine environment. Although transplantation has been recommended in some cases (Briggs 2008), it has yet to be attempted on a large scale. In highly modified harbors and estuaries the native biodiversity loss is often counteracted or exceeded by the invasion of exotic species. Although biodiversity per se may be relatively unaffected, the structure of the food web can be profoundly disturbed. Worldwide about 70% of local extinctions take place at high trophic levels (top predators), while a similar percentage of invasions are by species from lower trophic levels (macroplanktivores, deposit feeders, detritivores) (Byrnes et al. 2007).

CASE STUDIES

The consequences of food web changes caused by the substitution of exotic for native species can be illustrated by the historic changes that have taken place in the Wadden Sea, which extends along the coast of the Netherlands, Germany, and Denmark. It has been described as the world's largest intertidal system. Three large rivers introduce nutrients that support a high level of primary production. But the upper levels of the system have been severely depleted due to more than 2000 yr of human exploitation (Lotze 2005). Although 52 exotic species have restored much of the original biodiversity (Reise et al. 2005), the invaders are species that occupy the lower trophic levels. There are almost no more codfish, salmon, and sharks; the only remaining high-level predators are seals. The major commercial species remaining are shrimps, cockles, and blue mussels. None of the introduced species has eliminated a native species. Instead, the new arrivals have added to species diversity.

Although long-term environmental degradation is generally involved, overfishing often stands out as the immediate factor in the loss of species at the apex level and the trophic cascades that follow (Longhurst 2010). For example, the effects of the removal of predatory sharks by overfishing from estuaries along the western Atlantic coast were studied by Myers et al. (2007). The authors analyzed the survey data on the great sharks and the smaller elasmobranchs that formed their prey. All 11 species of great sharks exhibited significant population declines over the past 35 yr, ranging from 87% in sandbar sharks to 99% or more for bull, dusky, and smooth hammerhead sharks. Over the same period, analyses of the smaller prey revealed that 12 of the 14 species had significant increases in abundance. Among the largest was the approximate 20-fold increase in the abundance of the cownose ray *Rhinoptera bonasus.* Cownose rays consume shellfish of commercial value such as soft-shell clams, oysters, hard clams, and bay scallops.

The projected consumption of bivalves by the current population of cownose rays over 100 d of the summer occupation of Chesapeake Bay totaled 840000 metric tons (Myers et al. 2007). In contrast, the total harvest of bivalves for the same area was only 300 metric tons. The intense demand for bivalves by the exploding population of cownose rays illustrates a trophic cascade caused by the removal of the large sharks. Evidence from other parts of the world suggests that the great shark–ray–benthic mollusc trophic cascade is geographically widespread (Estes et al. 2010).

Considerable research has been devoted to 2 large areas that are sometimes described as semi-enclosed seas, even though they are estuarine in terms of their topography and freshwater input. Both the Baltic Sea and the Black Sea have suffered the decline of their top predators and have been invaded by lower-level organisms (Essington 2010). The Baltic supports 3 main commercial fisheries: cod, herring, and sprat. At present, cod is the apex predator, but cod populations are overfished and are still subject to very high fishing mortality. As cod populations dwindled, fishermen directed more effort toward the clupeid species, preferring the more valuable herring rather than the sprat. Over the past decades, herring populations have declined, but sprat populations have surged. Analysis of the trophic control of herring and sprat by cod (Essington & Hansson 2004) confirmed that the recent abundance of sprat was due to the relaxation of predation by cod. Recent research (MacKenzie et al. 2011) indicates that relationships among the 3 species may be complicated by the grey seal, a cod predator.

Alterations of the Black Sea ecosystem began with the overfishing of the large, piscivorous fishes which subsequently shifted to the smaller planktivorous fishes. The depletion of the latter coincided with outbursts of gelatinous zooplankton (Sorokin 2002). Daskalov et al. (2007) concluded that the early dynamics reflected a trophic cascade, but the recent dynamics reflect a different ecosystem where the gelatinous zooplankton and phytoplankton play a dominant role. The authors suggested that the Black Sea is in a state that might prevent recovery to historical conditions. This means that the Black Sea ecosystem may have entered into a new alternative state that is self-stabilizing. It is known that reversals from alternative states may be very difficult to achieve (Scheffer 2009).

The foregoing case studies indicate that estuarine invasions, together with the depletion or elimination of apex-level predators, constitute a global conservation problem. In estuaries, the effects of overfishing, pollution, and habitat degradation are often magnified because space is relatively limited. This means that native species suffer disproportionately and offer less opposition to invaders. These factors, plus increased propagule pressure from ship traffic, would account for the much greater numbers of invaders in estuaries compared to open coasts. There is often a striking contrast: in Elkhorn Slough, California, Wasson et al. (2005) identified 526 invertebrate species comprised of 443 natives, 58 exotics, and 25 cryptogens (species of unknown origin). The surrounding rocky intertidal open coast contained 588 species, of which only 8 were exotic and 13 cryptogenic. Similarly, more than 240 invasive species are known from San Francisco Bay, but fewer than 10 are found on the outer coast (Ruiz et al. 1997).

CONSERVATION

As recent research has demonstrated, trophic cascades have been reported in many other marine environments including intertidal habitats, coastal seas, open oceans, and the shallow tropics (Terborgh & Estes 2010). However, it is the highly modified and highly invaded harbors and estuaries that present the greatest conservation challenge. These relatively circumscribed areas generally exhibit the greatest environmental degradation, the highest loads of pollution, and the largest numbers of low-trophic-level invaders. As noted, the invaders, often represented by very large populations, should comprise an attractive food source for upper-level consumers. But the latter cannot thrive without pollution control, habitat improvement, and protection from overfishing.

If it is reasonable to concentrate our conservation efforts on those areas that have been most severely impacted by human activities, then harbors and estuaries, particularly those in temperate waters, should deserve a high priority. A practical solution that will benefit a given estuary is to adopt an ecosystem-based management program (Pauly 2009). This means that a significant area, as much as 50 % in the case of small bays, must be included in a no-take, marine protected area (MPA). In addition, the MPA should extend outward beyond the bay entrance to encompass part of the region utilized by migratory species that use the bay for part of their life cycles. With complete protection of an area that has ecological promise and where suitable habitat has been preserved or is restorable, we can begin to restore the original trophic structure. Once this work has started, and the ecosystem appears to be responding, the reintroduction of apex predators could be attempted. In the case of Chesapeake Bay, where there is also a bottom-up problem (Rooney et al. 2006, CBF 2008), there are available many filtering organisms resistant to pollution, such as some of those in San Francisco Bay (Carlton & Ruiz 2005), which could be transplanted to clear the water, promote benthic production, and to make the bay more suitable for human activities.

BODY SIZE IN PREDATOR SPECIES

Although managing for total species diversity remains important (Palumbi et al. 2009), much of recent ecosystem research has shifted to consideration of the effects of the loss or decline of individual species (Sala & Knowlton 2006). The depletion of species recognized as 'strong interactors', usually large predators, can reduce populations and biomass by orders of magnitude. There are many examples of such top-down effects that often result in trophic cascades affecting the entire food web. Small predators are usually considered to be 'weak interactors', but some small-sized species occur in very large numbers, which increases their food web impacts. Fish body size is an important factor in mediating the relationship between species richness and ecosystem functioning (Fisher et al. 2010)

Top vertebrate predators are large bodied and can move over large areas, thus coupling the dynamics of distinct communities (Terborgh et al. 2010). Also, the presence of large predators has importance beyond the prevention of trophic cascades. Work by Berkeley et al. (2004) indicates that larval viability varies with age and that the larvae produced by larger (older) adults have increased survival. For example, larvae produced by older female black rockfish *Sebastes melanops* grew more than 3 times as fast and survived starvation more than twice as long as did larvae produced by younger females. In addition, the older fishes were found to have a longer spawning season and possessed an exponentially greater fecundity.

As Birkeland & Dayton (2005) have observed, selective harvesting of older individuals leads to an exponential reduction in the number of larvae produced, a shortening of the reproductive season, a decrease in larval viability, and a selection for reproduction at a smaller size and younger age. In addition to these reproductive and genetic effects, the body size of fishes has consistently declined in response to fishing pressure, even in situations where total diversity (species richness) has remained high (Fisher et al. 2010). For example, in the northwest Atlantic, fish body masses have declined about 50% while species richness was little affected (Frank et al. 2007). Fisher et al. (2010) suggest that size-selective fishing may impact ecosystem functioning more rapidly and more profoundly than declines in species richness. The practical way to control size-selective fishing is to create effective MPAs so that individuals can grow to their optimum size and reproductive efficiency (Stobart et al. 2009).

CONCLUSIONS

From a biogeographic viewpoint, it is obvious that marine species on the world's continental shelves are constantly migrating, and that such movements are predominately from regions of high species diversity to those with less diversity. Investigations into the regional vs. local relationship have shown that this is also true at the community level. This natural and ongoing process of species invasions has been greatly augmented in certain places where many exotic organisms have been introduced by ship traffic. In such locations, the success of the invaders is primarily due to previous habitat destruction, pollution, and the overexploitation or displacement of the native species. A few of the invaders have become pests and a few have been beneficial, but the ecosystem effects of the great majority are unknown.

While it is true that ecosystems with greater species richness are generally more desirable, it is also true that diverse ecosystems in which the populations of top-level predators have been diminished or extinguished do not function well. So, in regard to the affected harbors and estuaries, large diversity increases at the lower trophic levels have limited benefits. Some estuaries also have bottom-up problems that are concurrent with lack of apex predators so that restoration needs to be initiated at the primary producer level. Conservation activities in harbors and estuaries tend to focus on habitat restoration and the detection and elimination of invader species. Although the former is certainly necessary, the latter, except for actions to prevent introductions by ships, is probably a waste of resources. It would be better to devote conservation efforts toward pollution control, habitat improvement, and restoration of the top-level predators. In the long run, a balanced ecosystem will be more resilient, productive, and resistant to invasion. Highly invaded localities such as the Wadden Sea, Black Sea, and Baltic Sea, have not sustained losses in overall species diversity, but they have endured the population collapse or loss of the large animals that are vital to ecosystem function.

Finally, it needs to be emphasized that the ultimate goal of estuarine management is the introduction or reintroduction of apex-level predators. Despite the major restoration projects that have been ongoing in the United States for the past 10 to 40 yr, none of them has resulted in improvements to the extent that the top trophic level could be resurrected. Yet recent research has provided ample evidence that healthy populations of large-size predators are essential to sustain balanced, productive marine ecosystems. Have we lost sight of this goal?

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