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OPINION
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Oyster Reef Restoration and Biological Invasions: An Overlooked or a Non-issue?

*Andrew A. David**

Biology Department, Clarkson University, Potsdam, NY, United States

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Edited by:
Liping Liu,
Shanghai Ocean University, China

Reviewed by:
Catherine Sarah Longo,
Marine Stewardship Council (MSC), United Kingdom

Correspondence:
Andrew A. David
adavid@clarkson.edu

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INTRODUCTION

Oyster reef restoration has become a popular method for combating biodiversity loss and environmental degradation in marine ecosystems, the latter of which includes the accumulation of pollutants, increased sedimentation and overall lowered water quality (Beck et al., 2011; Gilby et al., 2019). This is due to the suite of ecological functions that oysters carry out in their communities including but not limited to: (i) their role as foundational species providing habitats for organisms at various trophic levels (Coen et al., 2007), (ii) their renowned filtration capabilities which can improve water quality in historically polluted habitats (Coen and Luckenbach, 2000) and (iii) their ability to buffer against waves that cause erosion, thereby providing a natural engineering solution for shoreline protection (Morris et al., 2019). In practice, many oyster reef restoration projects have been promoted to address two overarching ecological problems: degraded water quality due to pollution, and fishery collapse. For example, Kellogg et al. (2013) found restored oyster reefs significantly increased denitrification and nitrogen sequestration rates in a river in Maryland, USA while in India, researchers are discussing the implementation of such reefs to mitigate nutrients and heavy metal pollution in coastal waters (Chakraborty, 2017). The structural complexity of overlaying beds of oysters also provides ideal recruitment sites for juvenile fishes and invertebrate larvae, while at the same time serving as foraging grounds for adults. In one study in coastal Louisiana, a direct assessment of fish and invertebrate biomass was carried out over 3 years after an oyster reef restoration project, and found that fish and invertebrate biomass was 212% greater when compared to local mud-bottom habitats (Humphries and La Peyre, 2015). In reflecting on the success of oyster reef restoration projects, one must also consider other effects that such projects may have on the immediately adjacent biotic communities. One potential side-effect could be the establishment of non-indigenous species (NIS) on the restored reefs. The goal of this opinion piece is to discuss how oyster reef restoration projects may serve as a gateway for alien marine species, and why a thorough taxonomic survey of fauna associated with restored reefs should be a required component of periodic reef-health assessments.

While most oyster reef restoration projects have occurred in habitats which had once historically supported oyster reefs, others have been deployed in regions where they did not historically occur. In both cases, the success of such projects, as determined by the presence of living oyster beds, is initially dependent on specific water quality parameters including salinity and turbidity, along with the presence of hard substrate for oyster larvae to settle and metamorphose (Morris et al., 2019; De Santiago et al., 2019). If first year recruitment is successful, then sustainability of the constructed reef will likely be dependent on the maintenance of the optimal water quality parameters in addition to long term connectivity of the new reef with other coastal habitats including other oyster and even coral reefs. Numerous successful reef restoration projects have been completed in various coastal systems, with most documented cases occurring in North America. For example, in the Gulf of Mexico, 73% of the artificial reefs constructed were considered "successful" (La Peyre et al., 2014), while in Virginia, more than 150 million native oysters were recruited over just 3 years as part of a long term restoration project (Schulte et al., 2009). Currently, an unprecedented project in New York Harbor, often considered as one of the most polluted waterways in the world, seeks to seed more than a billion oysters in the harbor to mitigate pollution and restore the vitality of this estuarine habitat (https://www.billionoysterproject.org).

OYSTERS AS VECTORS FOR NON-INDIGENOUS SPECIES

The transportation of aquaculture products, specifically shellfish, is one of the main vectors for the introduction of marine NIS around the world (Naylor et al., 2001). This is due largely in part to their shell architecture (e.g., the grooves and crevices of *Crassostrea gigas* and *C. virginica*) which provides microhabitats that can harbor a variety invertebrate species and algae. However, the potential for NIS establishment has rarely been addressed in oyster reef restoration studies, probably because the broad goal of enhancing biodiversity is the primary focus of these projects, regardless of whether NIS slips into the "restored" community. The construction of oyster reefs in a habitat without a historical legacy of oysters provides the best opportunity for invasions because oysters and their spat must be translocated from a different locality. Such translocations are notorious for delivering hitchhikers which can reside in mudpacks within the crevices of the oyster shell (e.g., juvenile crabs and amphipods), on the shell itself (e.g., encrusting species such as sponges, barnacles and anemone) and even within the shell (shell boring polychaetes) (Aikins and Kikuchi, 2001; David et al., 2014). Oyster shells, which are sometimes used to form the foundational hard substrate of the reef, may also harbor similar hitchhikers (Cohen and Zabin, 2009). Currently, there appears to be no checks on whether the oysters used for the initial seeding of reefs harbors NIS. In addition, if juveniles fail to recruit in the initial phase of the project, then additional translocation of oysters would have to occur to spur recruitment (Geraldi et al., 2013), which in turn would increase propagule pressure of NI hitchhikers. In the invasion biology literature, propagule pressure refers to the number of individuals released into a habitat where they are non-native and incorporates both (1) absolute number of NI individuals released in single event and (2) the number of independent release events.

While not all introduced species become invasive, those that do can displace native species, alter the geophysical and chemical environment and in doing so, severely disrupt ecosystem functioning (Molnar et al., 2008). The invasion potential of a NIS is dependent on several factors including the specific species involved, the type of marine ecosystem being invaded and perhaps most importantly, the degree of habitat disturbance and degradation. Severely disturbed habitats are particularly vulnerable because alien species may already be present but kept in check due to the lack of optimal abiotic (e.g., water quality) and or biotic (e.g., settlement sites) factors. As an example, consider spionid polychaete worms which are capable of burrowing into the shells of molluscs as juveniles, which they then reside in for the rest of their adult lives (Blake, 1969). These worms are notorious pests of commercially reared shellfish especially oysters and abalone, and when present in high intensities, can negatively affect the profitability of shellfish farms by weakening the host shellfish and stunting its growth (David et al., 2014). Most of these shell-boring worms produce planktrophic larvae that spends a lengthy time (up to 30–40 days) in the water column and therefore can be taken up into ballast water (David and Simon, 2014). However, their establishment in a new habitat is largely dependent on the presence of appropriate calcareous substrate for settlement (David et al., 2014). For example, the obligate shell borer, *Polydora hoplura* can inhabit coralline algae and barnacles, however if provided with oyster stocks, can proliferate rapidly in a relatively short period of time due to a preference for this substratum (David, 2015). This is one of the reasons why the heaviest infestations are often seen in farmed environments where oysters are cultivated in high densities (analogous to a reef setting). In other words, the construction of oyster reefs has the potential to reduce the lag phase of the invasion process.

Fortunately, a growing number of regulatory bodies have begun to seriously consider the problem of invasions as an important biosecurity issue that must be factored into the early stages of reef restoration planning (see Pogoda, 2019 and references therein). For example, in the North Sea, researchers and planners have recommended that to avoid the translocation of alien species, seed oysters should preferably be sourced from hatcheries rather than from wild stocks and if they must come from the latter, there should be a quarantine period prior to introduction and or the oysters should be chemically treated to eradicate any hitchhikers (Sas et al., 2019). However, hatchery raised oysters can also be hosts to alien species, especially if unfiltered water is being pumped in directly from the ocean (Williams et al., 2016). Furthermore, chemical treatment of seed oysters may only be effective against some hitchhikers while others may exhibit a greater degree of physiological tolerance to the treatment. I therefore propose that thorough taxonomic surveys of reef fauna be carried out intermittently as part of periodic reef health assessments during the restoration period. Currently, health assessments of a restored reef amounts to focusing primarily on water quality changes and the percentage cover of living oysters. Periodic surveys that emphasize finer taxonomic resolution have the power of detecting alien species early in their establishment phase, which allows for faster and more targeted eradication (David and Krick, 2019). Faunal surveys are typically carried out only after a reef has been restored and because the data collected is used primarily for calculating species richness and diversity, taxonomic integrity is not necessarily a requirement i.e., common names are sometimes used and identification to Genus or even Family rank is considered acceptable (see Blomberg et al., 2018). Taxonomic integrity is critical because there have been numerous instances of "cryptic invasions" in coastal habitats, where a NIS goes undetected due to misidentification with either a native species or another NIS (Morais and Reichard, 2018). To address this issue, DNA barcoding can be deployed in such surveys for rapid and accurate detection as has been done in previous biodiversity surveys (Saunders, 2009; David and Krick, 2019). Furthermore, recent improvements in using eDNA analyses to assess community variation (West et al., 2020) would eliminate the need for frequent disruption of the reef to sample for organisms. While taxonomically intensive biodiversity surveys may add to the cost of a reef restoration project, especially if it involves recruiting specialists, restoration ecologists should also consider that the cost of dealing with an invasion event because an NIS was not detected earlier, would likely be significantly higher.

CONCLUDING THOUGHTS

Finally, it should be emphasized again that not all NIS introduced into a new habitat become invasive—indeed, most do not. In one interesting example, surveys of a restored oyster reef in the Dutch coastal area of the North Sea found that native oysters (*Ostrea edulis*) increased in population size by using the invasive *Crassostrea gigas* seeds as a settlement substrate (Christianen et al., 2018). Nevertheless, if the overarching goal of oyster restoration projects are to protect or enhance ecosystems, then any potential invasion event still poses a serious risk to accomplishing such a goal and efforts to prevent the introduction of NIS must be prioritized in the planning process.

AUTHOR CONTRIBUTIONS

AD devised the idea of this opinion piece and wrote the article himself.

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