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REVIEW
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Artificial Reefs in the Northern Gulf of Mexico: Community Ecology Amid the “Ocean Sprawl”

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The northern Gulf of Mexico has been an important source for crude oil and natural gas extraction since the 1930s. Thousands of fixed platforms and associated equipment have been installed on the Gulf of Mexico continental shelf, leading to a pervasive ‘ocean sprawl.’ After decommissioning, 100s of these structures have been converted to artificial reefs under the federal ‘Rigs-to-Reefs’ program, in addition to artificial reefs specifically designed to enhance fisheries and/or benefit the recreational diving industry. Apart from a few natural banks, which reach to approximately 55 ft below the surface, artificial reefs provide the only shallow-water hard substrate for benthic organisms in the deeper waters of the northern Gulf of Mexico. This vast expansion in available habitat has almost exclusively occurred over a relatively short span of time (∼50 years). The ecological interactions of artificial and natural reefs in the northern Gulf of Mexico are complex. Artificial reefs in general, and oil and gas structures in particular, have often been invoked as stepping stones for non-native and invasive species (e.g., *Tubastrea* cup corals, lionfish). The pilings are covered with fouling communities which remain largely unstudied. While the risks of these fouling organisms for invading natural reefs are being broadly discussed, other impacts on the ecological and economic health of the Gulf of Mexico, such as the potential to facilitate jellyfish blooms or increase the incidence of ciguatera fish poisoning, have received less attention. Artificial reefs also provide ecosystem services, particularly as habitat for economically important fish species like red snapper. Here we revisit the potential role of artificial reefs as ‘stepping stones’ for species invasions and for fisheries enhancement. Beyond concerns about ecological effects, some of these topics also raise public health concerns. We point out gaps in current knowledge and propose future research directions.

Keywords: oil and gas platforms, red snapper, lionfish, regal demoiselle, *Tubastrea*, jellyfish blooms, ciguatera, fouling communities

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INTRODUCTION

The northern Gulf of Mexico (nGoM) is home to nearly 2,200 active oil and gas platforms (BSEE/BOEM Data Center, 2019). In addition, there are almost as many artificial structures not currently used for oil or gas extraction, including ‘reefed’ oil and gas platforms, submerged vessels, reef balls and others (**Figure 1**; Broughton, 2012). These-human made structures create so-called 'ocean sprawl' (Duarte et al., 2013; Firth et al., 2016), altering the habitat by creating hard substrate, forming barriers to movement for some organisms and changing predator-prey interactions (Bishop et al., 2017). In 2016, the total number of artificial reefs in the nGoM (including active and inactive) amounted to 4,176 (NOAA, 2016).

Before oil and gas exploration, the seafloor was mostly sedimented, although the bathymetry of the continental slope is complex and frequently marked by domes, pockmarks, canyons, faults, and channels. The nGoM is additionally home to some of the best studied cold seep communities in the world (e.g., Fisher et al., 2007; Cordes et al., 2009) as well as coral banks and reefs. Known coral assemblages in the GoM range from phototrophic in the shallower portions to mesophotic and deep coral communities, down to more than 2,500 m in De Soto Canyon (Doughty et al., 2014). Shallower coral assemblages are often present on artificial structures (Bright et al., 1991; Sammarco et al., 2014a).

Near the edge of the continental slope off the coasts of Texas and Louisiana, multiple banks formed by underlying salt diapirs support natural reefs. The best known of these are the East and West Flower Garden Banks, which constitute the core of the Flower Garden Banks National Marine Sanctuary (FGBNMS). The Flower Garden Banks are not only the northernmost coral reefs of the greater Caribbean but also the most isolated and among the healthiest with regard to coral cover (Hickerson et al., 2012; Johnston et al., 2016a). Located within the sanctuary boundaries, High Island 389A (HI-389A) is a decommissioned platform installed in 1981 located on a 20-acre artificial reef site in a water depth of 410 feet (**Figure 2**). The structure has recently (July 2018) been reefed by removal of the top 65 ft below the water line. The FGBNMS further includes Stetson Bank, located closer to the shore. The FGBNMS Advisory Board recently voted to expand the sanctuary boundaries to include 14 additional banks. Approximately 150 platforms are located within 25 miles of the current sanctuary borders (US Department of Commerce, 2012). The proposed new boundaries as set out in the Sanctuary Expansion DEIS will incorporate three additional oil and gas production structures.

Natural and artificial reefs are interspersed with each other in the nGoM. This network of habitable 'islands' separated by stretches of uninhabitable (or less preferred) ground, provides unprecedented opportunities for organismal movement between these two habitat types. In this context, the geographic isolation of the FGB is a double-edged sword. On the one hand, it may provide relative protection from some dangers that threaten other Caribbean reefs, such as coral pathogens, nearshore anthropogenic impacts, and invasive species. On the other hand, isolation may hinder recruitment and adult replacement, especially after cases of local coral mortality. Despite isolation, some invasive species, most notably lionfish, have become established at the FGB (Johnston et al., 2016b). Oil and gas structures and other artificial reefs are often regarded as 'stepping stones' for invasives (Fenner, 2001; Sammarco et al., 2004, 2012a). However, this stepping-stone theory is ecologically complex, as much of the fauna on platforms is a typical 'fouling community' as opposed to a true reef community (Page et al., 2010). For example, artificial structures are more often dominated by small, flexible hydroid colonies rather than reef building corals. However, some species overlap between the two habitat types does exist. Utilization of these different habitat types by organisms with different life histories and ecological characteristics has far-reaching implications for marine conservation as well as commercial and recreational fisheries.

Previous reviews on the ecological roles of artificial reefs either had a national (Broughton, 2012) or global (Bull and Love, 2019) scope. The purpose of this review is to focus on the nGoM and summarize our current state of knowledge of the habitat preferences of different organismal groups inhabiting artificial reefs as well as functional connectivity between artificial and natural reefs. We will discuss the implications of the existing knowledge for ecosystem health and society, and identify knowledge gaps and future research directions.

Functional connectivity is here defined as the movement of organisms or particles among different locations or habitats (Bishop et al., 2017). When focusing on populations of individual species, the term population connectivity is used; multiple connected populations form a metapopulation (Cowen and Spunaugle, 2009). We consider the area offshore from the coasts of Texas, Louisiana, Mississippi, Alabama and Florida between approximately longitude 97° and 81° W and latitude 24° and 30° N (**Figure 1**). This area mostly encompasses the coastal areas to the continental slope, with a maximum depth of about 3,000 m. The review does not cover the effects of platform installation, operation and removal on soft sediment benthic communities, or the toxicological impacts of accidental spills or produced water, as these aspects have been reviewed elsewhere (e.g., Broughton, 2012; Cordes et al., 2016).

Prior reviews on connectivity between natural and artificial reefs in the nGoM were generally focused on particular taxonomic groups, such as corals (e.g., Sammarco et al., 2004) or commercially important fish (e.g., Shipp and Bortone, 2009; Cowan et al., 2011). This review has a wider taxonomic scope and broader view of ecological implications, in particular highlighting emerging concerns for which we lack sufficient knowledge. In light of the continuing proliferation of artificial reefs in the region, ongoing fisheries trends and the recent detection of previously unreported species (e.g., Bennett et al., 2019; Figueroa et al., 2019), this review is timely and can serve as a baseline to evaluate future developments. It is our hope that the information provided will guide future research efforts and management decisions.

CONNECTIVITY: STEPPING STONES, METAPOPULATIONS, RESILIENCE, AND REPLACEMENT

Connectivity and resilience in dispersal networks are generally correlated, as more densely connected habitats are more likely

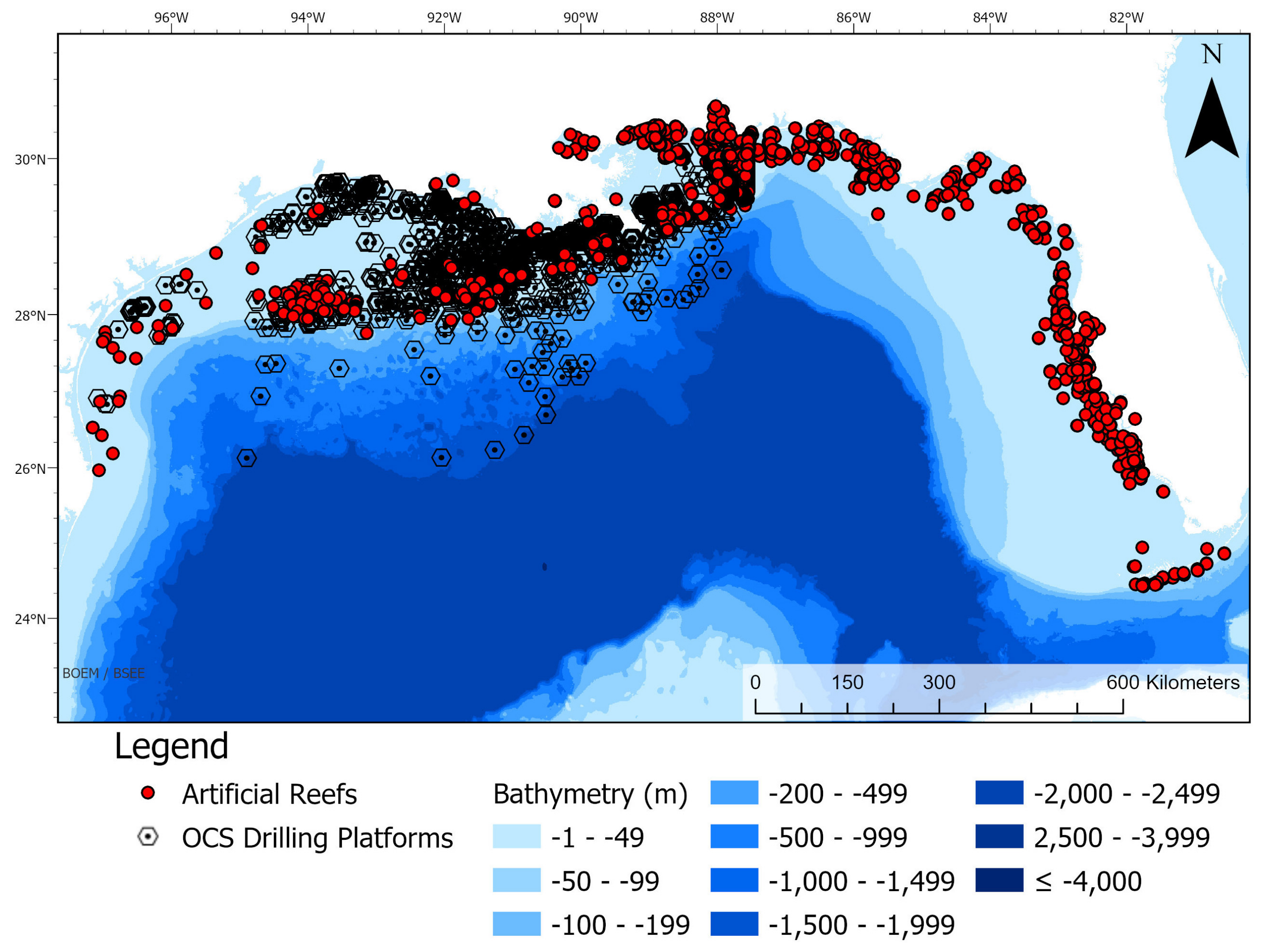

FIGURE 1 | Total artificial reefs of nGoM (red) and outer continental shelf drilling platforms (black) shown with bathymetry in meters. Data from NOAA (2016) and BSEE/BOEM Data Center (2019).

to avoid recruitment failures. The 1000s of artificial structures in the GoM expand the habitats for naturally occurring (Sammarco et al., 2004, 2012b; Kolian et al., 2017), invasive (Fenner and Banks, 2004; Sammarco et al., 2012b; Dahl and Patterson, 2014), and fouling communities in the region, and simultaneously increase the density of the dispersal networks of these communities.

The metapopulation effects of artificial structures have been investigated in other coastal oceans, and support the notion that these structures support benthic, epibenthic, and migratory communities in complex ways. Paxton et al. (2019) found that artificial reefs on the subtropical US Atlantic continental shelf disproportionately support highly mobile tropical planktivorous and piscivorous fishes when compared to natural reefs, and they expand the biogeographic ranges of those species into higher latitudes. In the North Sea, artificial structures can increase the resilience of threatened coral species, both within the connected communities on artificial structures, as well as in nearby naturally occurring communities (Henry et al., 2018). It is reasonable to assume that artificial structures in the GoM increase metapopulation resilience for a diverse set of species – including historical natives, native and non-native invaders, and those species unique to fouling communities.

However, artificial structures are inherently more ephemeral than most naturally occurring comparable habitats in the nGoM. These structures are routinely decommissioned and subsequently removed, or reefed. Even when reefed, artificial structures and associated communities may undergo physical degradation and/or community succession (Sammarco et al., 2014a), which suggests the populations found on artificial structures are dynamic in both space and time. Metapopulation resilience is sensitive not only to the density of the dispersal network, but also to the rates of colonization and extinction at individual patches (Hanski and Ovaskainen, 2000). Thus, the assumed density of connectivity among artificial structures must be weighed against these rates when assessing the persistence of metapopulations supported by artificial structures. To date, rates of colonization, extinction, and larval connectivity among artificial structures in the GoM are not well-understood; however, data are available on the rates of decommissioning of artificial structures, which could help to inform the persistence of these unique communities.

As noted elsewhere in this review and in previous studies, the artificial structure communities in the GoM are not identical to, and not entirely different from, adjacent natural habitats. The hypotheses are usually that, following local extinctions on natural habitats, recolonization may occur with larvae from nearby artificial structures (Sammarco et al., 2012b), or that fouling communities will not establish on naturally occurring hard substrates. Although invasives that occupy artificial structures are routinely found on the FGB (e.g., *Tubastrea coccinea*, Fenner and Banks, 2004), a possibility that has not been fully addressed to date is that invasive or competitive species that occupy artificial structures could supplant naturally occurring species on natural habitats following perturbation or local extinction. A specific example may be the potential for alternative stable states between coral and sponge communities (reviewed in Norström et al., 2009). Sponges of the genera *Cliona* and *Chondrilla* have been shown to supplant hard corals following coral mortality events and prevent the recolonization of coral. Sponge communities on artificial structures in the GoM can be diverse (Rützler et al., 2009), but the distributions of sponges in those genera on artificial structures is not currently known. Following a perturbation to the coral communities on the FGB, colonization from sponge communities on nearby artificial structures may be more likely than colonization of hard corals from reefs that are further away.

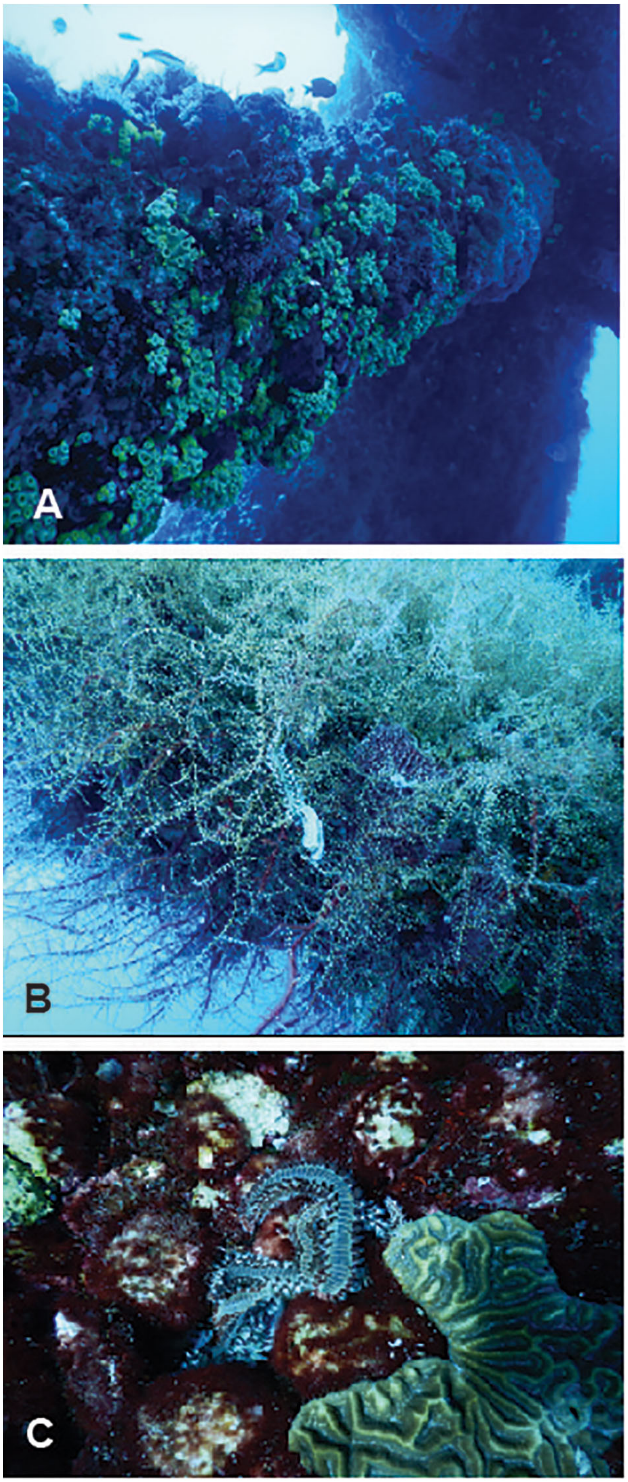

FIGURE 2 | Examples of the fouling community and associated motile fauna on High Island 389A (HI-389A). **(A)** Numerous colonies of *Tubastrea coccinea* shown on the underside of a horizontal beam of at 37 m. **(B)** The hydroid, *Thyroscyphus* sp., with a bearded fireworm, *Hermodice carunculata*, on top on a diagonal structure support beam on HI389-A at 20 m. **(C)** Five bearded fireworms, *H. carunculata*, in close proximity to a scleractinian coral (*Pseudodiploria strigosa*) on a horizontal beam of HI389-A at 9 m.

Fouling Communities

Fouling communities, defined as assemblages of sessile organisms and associated species with limited mobility growing on human-made structures, are vastly understudied on offshore artificial structures in the GoM. The term 'fouling community' has a negative connotation, implying that these organisms are unwanted and destructive. On vessel hulls, sessile organisms increase drag and thereby reduce vessel speed and fuel efficiency. On oil and gas platforms, fouling communities can greatly increase the weight of the structure, as well as the diameter and surface roughness of the platform members (Page et al., 2010) (**Figure 2**), affecting the hydrodynamic loading of the platform and interfering with visual inspection. However, fouling communities on platforms provide ecosystem services, as prey items and ecosystem engineers of complex habitat for other sessile and motile organisms (Daigle et al., 2013), including commercially important fish species. The establishment of fouling communities is largely driven by the relative concentrations of propagule stages present in the water column but varies depending on many physical characteristics, such as light, temperature, salinity, pressure, spatial orientation and current regimes, as well as the interactions between biotic and abiotic factors (Terlizzi and Faimali, 2010).

As the vast majority of oil and gas platforms worldwide are constructed in soft substrate, the fauna on the structure tends to be inherently different from the surrounding benthic fauna. However, even if platforms are erected in the vicinity of natural hard substrates, the fouling fauna is generally distinctive (Page et al., 2010). This may be a result, in part, of the structure reaching from the seafloor to the surface allowing for increased primary producer activity and bioaccumulation in a location where it would not otherwise be possible (Daigle et al., 2013). Regardless, artificial structures expand the habitat of distinct fouling communities into areas of both soft and hard substrates on the continental shelf of the GoM.

On oil and gas platforms, shallow fouling communities are generally dominated by a few taxa with hardened shells. In the GoM barnacles tend to dominate the nearshore structures, whereas bivalves are more prevalent on offshore structures, in addition to extensive growth of hydroids (**Figures 2B**, **3**) (Lewbel et al., 1987; Bull and Kendall, 1994; Page et al., 2010).

These structures can become colonized and integrated into fouling metacommunities fairly rapidly. Nearly 1 year after the installation of HI-389A, surveys were conducted from the surface to the 37 m horizontal supports and describe the establishment of fouling mats with hydroids and macroalgae (Boland, 2000). Bearded fireworms (*Hermodice carunculata*) and two species of sea urchin (*Diadema antillarum* and *Arbacia punctulata*) were present in noticeable amounts at this time (Boland, 2000). Hermatypic corals were also recorded on HI-389A in 1990, 9 years after installation, supporting the idea that these rigs provide settling surface for reef-builders (Boland, 2000).

Documented Invasions

There is an ongoing debate whether artificial reefs in the nGoM act as 'stepping stones' for non-indigenous or invasive species. In most cases, there is no definitive answer as to whether a non-indigenous species would be present in the area if there were no artificial reefs. Knowledge of a species' life history and its behavior in other regions can provide some insight about the invasion history and may guide future management decisions. Here we review the evidence for a few non-indigenous taxa and their presence on natural and artificial structures in the nGoM.

Lionfish

Two species of Indo-Pacific lionfish, the red lionfish (*Pterois volitans*) and the devil firefish (*Pterois miles*) are established throughout the Caribbean, and their detrimental effects on native fauna are well documented (reviewed in Albins and Hixon, 2013; Côté et al., 2013). *P. volitans* and *P. miles* are morphologically similar and can only be distinguished by different numbers of dorsal and caudal spines, but their distinct genetic signatures confirm them as separate species, with *P. volitans* representing 93% of the sequenced specimens (Hamner et al., 2007). Genetic diversity within each species is low, indicating single, rapid invasions (Hamner et al., 2007).

Lionfish were first sighted in the nGoM in 2010 (Nuttall et al., 2014). By 2013, their numbers had increased exponentially on both natural and artificial reefs, but their densities on artificial reefs were two orders of magnitude higher and they exhibited a more varied diet than on natural reefs (Dahl and Patterson, 2014). Their rapid growth rates suggest that biomass is increasing even more rapidly than the numbers of individuals (Dahl and Patterson, 2014).

Some contributing factors to the success of *Pterois* spp. in the GoM include: buoyant egg masses and long-lived larvae [28 days (Ahrenholz and Morris, 2010; Morris et al., 2011)], limited number of natural predators (Mumby et al., 2011; Diller et al., 2014), rapid growth rate (Green et al., 2011), and high reproductive success (Albins and Hixon, 2013). Fogg et al. (2017) examined the reproductive biology of *P. volitans* in the nGoM. Comparative reproductive data from the native range of the species are surprisingly sparse, but it appears that reproductive output is higher in the nGoM than in the native range.

NOAA, partnering with several other organizations, has been conducting annual 'Lionfish Invitationals' since 2015 to document and capture lionfish in the FGBNMS. While this effort will greatly contribute to the scientific study of lionfish in the nGoM, it likely does not significantly reduce their populations. Nuttall et al. (2014) detected nearly 400 lionfish, including both species, in mesophotic environments down to 112 m on 14 banks surveyed by ROV, with the highest counts between 80 and 90 m depth. At the time of the study, the eastern banks were more heavily invaded than the western banks. Three of the western banks (Horseshoe Bank, 29 Fathom Bank and Bright Bank) seemed to still be free of lionfish.

Paxton et al. (2019) provide indirect support that artificial reefs have contributed to the lionfish invasion in the nGoM. Their survey of fish abundance and diversity on 30 artificial and natural reefs off the coast of North Carolina show that tropical fish at their distribution edge, particularly planktivorious and piscivorous species, have higher abundances on artificial than on natural reefs. They conclude that artificial structures probably act as stepping stones for northward expansion of motile tropical fish species in the face of climate change.

The Regal Demoiselle, *Neopomacentrus cyanomos*

This small (<10 cm) species of damselfish is the latest documented newcomer in the nGoM, including the FGBNMS (Bennett et al., 2019; Nuttall et al., 2019). The Indo-Pacific/Indian Ocean species was first reported from natural reefs in the southern GoM off the coast of Veracruz in 2013 (González-Gándara and de la Cruz-Francisco, 2014). Johnston and Akins (2016) modeled the invasive potential of this species and concluded that currents in the southern GoM were not conducive to long-distance transport of *N. cyanomos* larvae. Nonetheless, around the same time, *N. cyanomos* was reported from Cayo Arcas on the southwestern corner of Campeche Bank, ca. 350 km distant from the original sighting (Robertson et al., 2016). In this area it was reported as 'superabundant' on the coral reef as well as on an oil platform which housed 'thousands' of individuals (Robertson et al., 2016). Subsequent reviews of video footage showed that the species was already present in 2013, but remained unrecognized at the time (Robertson et al., 2016).

In 2017, Bennett et al. (2019) surveyed 138 sites, including natural and artificial reefs, off the Alabama coast. While no *N. cyanomos* were sighted on natural reefs, several hundred of

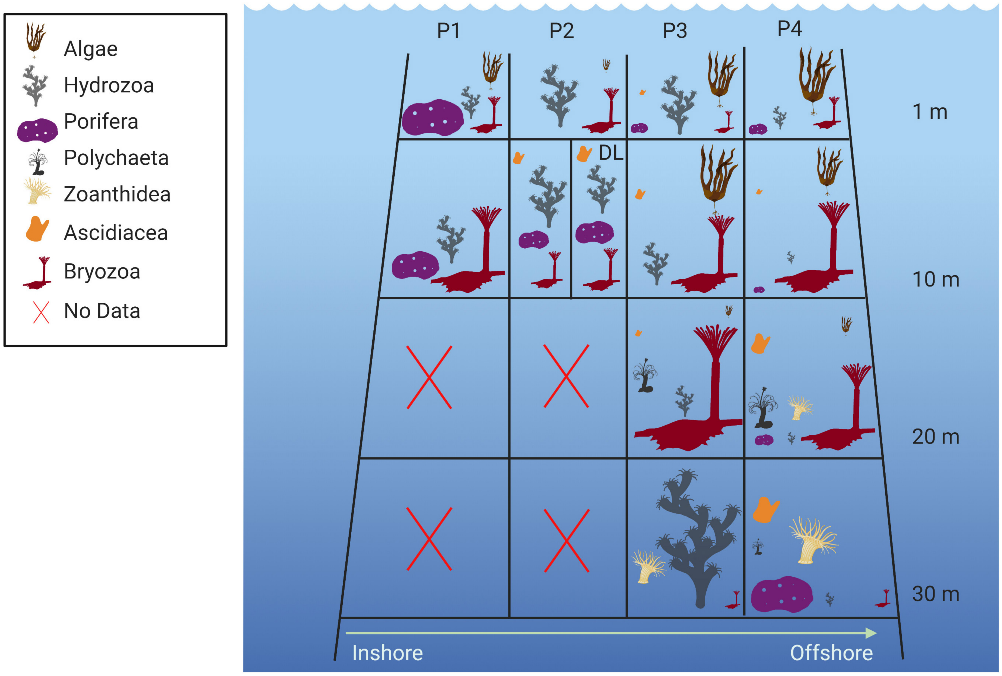

FIGURE 3 | Zonation of fouling communities on four platforms (P1–P4) off the Louisiana coast from Lewbel et al. (1987). The size of the respective symbols represents the relative contribution of the taxon to the percent cover. The platforms were located in 12 to 46 m of water and fouling communities were sampled at 1 and 10 m depth at all platforms and additionally at 20 and 30 m depth at P3 and P4. At P2, an additional sampling station (P2-DL) was established above a produced water outlet. Note that scleractinian corals were not sampled on P1–P4 but were reported (but not quantitatively sampled) from other platforms in the area.

the non- native damselfish were discovered in groups of 10–35, primarily juveniles, on five petroleum platforms and one concrete structure. It is unclear whether they reached these locations via ship ballast water (the Ports of Mobile, AL and Tampico, Veracruz are well-connected through shipping routes) or whether early life stages may have been transported there via the Loop Current. Although it was initially uncertain whether *N. cyanomos* would be able to survive the colder winter water temperatures in the nGoM, Bennett et al. (2019) confirmed their presence in 2018. In late June, 2018, NOAA reported the presence of *N. cyanomos* at Stetson Bank where schools of several 100 individuals were observed on multiple pinnacles and inside sponges (Nuttall et al., 2019). The ecological impact of this most recent invasion is difficult to predict, but the possible displacement of native damselfish species is a concern.

Cup Corals: *Tubastrea* spp.

Tubastrea coccinea, also known as the orange cup coral, is an Indo-Pacific non-zooxanthellate scleractinian stony coral (Sheehy and Vik, 2010) which was introduced to the Caribbean in 1943 and in the GoM in the 1960s. It now has a pantropical distribution and is considered the most abundant scleractinian species in both the tropical Pacific and Atlantic (Cairns, 1994). A second species, the green cup coral *Tubastrea micranthus*, was first detected in 2006 on a single platform (GI-93-B) off the coast of Louisiana (Sammarco et al., 2010), but had appeared on eight additional platforms within a 20 mile radius of GI-93-B by 2014 (Sammarco et al., 2014b). The two species show clear depth preferences: whereas *T. coccinea* is generally found above 78 m, *T. micranthus* occupies deeper portions of the platforms, down to 138 m (Sammarco et al., 2013). Recently, a third species, the Indo-Pacific *T. tagusensis,* has been reported for the first time on offshore plantforms in the GoM (Figueroa et al., 2019). Although sampling was limited, in some sites *T. tagusensis* seemed to outnumber *T. coccinea*. Morphologically, *T. tagusensis* is very similar to *T. coccinea,* and although it can be distinguished from its congener using molecular tools, misidentification of *T. tagusensis* as *T. coccinea* may have occurred in the past. This complicates attempts to understand the history and timing of *T. tagusensis* GoM invasion. If *T. tagusensis* has only recently invaded the GoM, Figueroa et al. (2019) argue it may be expanding rapidly and potentially outcompeting *T. coccinea*, thus posing a new threat to the GoM ecosystems.

Tubastrea coccinea exhibits a predominantly hermaphroditic reproduction, with typical non-feeding cnidarian larvae, planulae that settle on the appropriate substrate after 1 to 3 days. However, the planulae can survive and be competent for up to 100 days (Fenner, 2001), thus showing massive potential for dispersal. *T. coccinea* has multiple reproductive cycles per year, and can also reproduce asexually, all traits that generally favor invasive species success. Assemblages of *T. coccinea* have been reported fouling hulls of boats (Cairns, 2000) and the species is believed to have been introduced by shipping. In the GoM, after being reported on oil and gas platforms, it was reported on a range of human-made structures, such as sunken vessels and other artificial reefs (Shearer, 2009). Although there is evidence that *T. coccinea* takes advantage of newly formed habitat, it can sometimes be found on established reef communities, including in the FGBNMS. Removal experiments in the FGBNMS have shown that *T. coccinea* has a very rapid recolonization rate (Precht et al., 2014). Off the coasts of Mexico, Texas, and Louisiana, it has been shown to colonize artificial reefs and oil rigs within a few years of their installation (Fenner, 2001) and it has been rapidly expanding its invasive range (Creed et al., 2017). On oil and gas platforms in the nGoM, *T. coccinea* is most abundant in relatively shallow waters, peaking at about 17 m (Sammarco et al., 2004), although it can be found at deeper sites (Sammarco et al., 2013). Its depth distribution may be limited by environmental factors such as sedimentation and turbidity associated with river discharge (Sammarco et al., 2013).

Tubastrea coccinea is an excellent competitor for space and, in parts of its invasive range, it has been shown to outcompete local coral species (Creed, 2006; Lages et al., 2011; Riul et al., 2013) and cause tissue necrosis to colonies that come in contact with its polyps (dos Santos et al., 2013). It can also impact mussel beds (Mantelatto and Creed, 2015), and alter local community structure and biodiversity (Lages et al., 2011).

Acorn Barnacles

Anthropogenic transport of acorn barnacles (Cirripedia) probably dates back many centuries, as they are some of the most common fouling organisms on ship hulls. Additionally, their nauplius larvae are long-lived and able to survive long passages in ballast water (Cohen et al., 2014). As such, the native distributions of most species are hard to determine and species are often characterized as 'cryptogenic' (of unknown geographic origin). Like many other fouling organisms, most barnacle species are difficult to identify, especially because many characteristics of their shell and appendages can be plastic depending on environmental conditions (Cohen et al., 2014). Carlton et al. (2011) list four non-native species of barnacles in the GoM and reconstruct their invasion history. In chronological order, the four species are *Balanus trigonus*, *Amphibalanus amphitrite*, *Amphibalanus reticulatus,* and *Megabalanus coccopoma*. *B. trigonus* has been established the longest, probably introduced in the mid- to late 1800s on ship hulls and is now abundant throughout the nGoM (Gittings, 1985; Carlton et al., 2011). The two *Amphibalanus* species first appeared in the 1950s (Carlton et al., 2011). *M. coccopoma* is native to the eastern Pacific and was first reported in the GoM by Perrault (2004) from jetties in Louisiana. *M. coccopoma* is a large barnacle with a characteristically pink shell. Cohen et al. (2014) examined mitochondrial sequence divergence in this species throughout its native and invasive range. Their study revealed that there were likely multiple invasions in the Southeastern US and Brazil. The species is now common on oil and gas structures (Gittings, 2009). Other *Megabalanus* species may be established in the GoM as well.

The environmental implications of introduced barnacles are not well-understood because there are often no baseline data from before the invasion. Large barnacles like *M. coccopoma* may be particularly successful in competing with smaller species, as they are able to occupy space faster and possibly filter feed more efficiently. Fouling by large barnacles on artificial structures can also add substantial weight and volume to a structure and affect its hydrodynamic properties. The survival and northern expansion of the tropical *M. coccopoma* may be limited by water temperature (Crickenberger et al., 2017), but warming temperatures may facilitate its northward spread in the future.

Tunicates: *Didemnum perlucidum*

The invasion history of the colonial tunicate, *Didemnum perlucidum,* in the GoM remains poorly documented. Culbertson and Harper (2002) report that between 1998 and 2000, divers observed a thin white layer of this encrusting species that almost completely covered structure High Island A-532 from 27 m to least 42 m depth (the depth limit of the SCUBA surveys). High Island A-532 is located 12 nautical miles from Stetson Bank (part of the FGBNMS) in 58 m of water and was installed as an artificial reef in 1997. *D. perlucidum* was also observed on several nearby structures within 12 nautical miles (Culbertson and Harper, 2002). The species can be characterized as cryptogenic. It was originally described from the island of Guadeloupe (Monniot, 1983), but it is uncertain whether its native range included the Caribbean. *D. perlucidum* is distributed worldwide in tropical and subtropical waters and is most prevalent on artificial structures (Dias et al., 2016). Its most recent appearance has been in Western Australia where it was first detected in 2010 and has since spread to the Northern Territories (Smale and Childs, 2012; Bridgwood et al., 2014; Dias et al., 2016). Ascidians have very short-lived larval stages, and introductions are therefore likely a result of the propagation of adults from fouling communities on boat hulls or rafting debris. Dias et al. (2016) studied genetic diversity of *D. perlucidum* worldwide, including a population from the GoM (Veracruz, Mexico), using cytochrome *c* oxidase subunit I (COI) sequence data. They found that genetic diversity is low, with a single haplotype (Haplotype 1) present in most locations. This likely indicates that most of the populations are relatively recent introductions. However, as *D. perlucidum* reproduces both sexually and asexually through budding, the genetic uniformity may be partially attributable to clonal organization. The GoM population actually included Haplotypes 1 and 3 but it is unclear whether the two haplotypes represent two separate introductions or local speciation. More sensitive molecular markers are needed to resolve finer scale population differentiation for this species.

EMERGING CONCERNS

Artificial reefs may not only provide habitat to newly arriving species, but may also promote habitat-limited native species which could lead to shifts in trophic structure and ecosystem function in the Gulf of Mexico. Furthermore, some of these species, notably jellyfish and *Gambierdiscus* species dinoflagellates, may raise public health concerns if their abundance increases, as is likely under predicted climate change scenarios.

Implications of Oil and Gas Structures for Jellyfish Blooms

Jellyfish (Scyphozoa, Cnidaria) go through seasonal pulses in response to environmental triggers, and rapidly produce enormous biomass that impacts the marine food chain. Three jellyfish species have formed massive blooms in the GoM: the moon jelly, *Aurelia* sp. 9; the Atlantic sea nettle, *Chrysaora quinquecirrha,* and the Australian spotted jellyfish, *Phyllorhiza punctata* (Graham, 2001; Robinson and Graham, 2013; Chiaverano et al., 2016; Frolova and Miglietta, 2020). Patches of *P. punctata* covering up to 150 km and composed of an estimated 5.6×10^6 medusae have been reported. These super swarms threaten large commercial fisheries and can cause millions of dollars in damage (Graham et al., 2003).

In contrast to the relatively large pelagic medusa stages, the benthic scyphozoan polyps are microscopic and have never been detected in the GoM. Because most of the naturally available benthic habitat in the GoM is soft sediment and unsuitable for polyp attachment, it has been hypothesized that the polyps have successfully colonized artificial substrates, such as oil and gas platforms (Graham et al., 2003; Duarte et al., 2013). A recent body of literature indicates that artificial substrates, including oil and gas platforms, are suitable substrate for scyphozoan polyps (van Walraven et al., 2016; Dong et al., 2018) and play an important role in the frequency and magnitude of jellyfish blooms (Duarte et al., 2013). Moreover, there is evidence that the removal of artificial structures may limit jellyfish bloom occurrence (Jin et al., 2017) and that artificial platform-originating planulae (cnidarian larval stage) play an important role in sustaining local jellyfish populations (Vodopivec et al., 2017).

Occurrence of Ciguatera Toxin-Producing Dinoflagellates

The complex fouling communities on artificial structures also represent potential habitat for benthic/epiphytic dinoflagellates of the genus *Gambierdiscus*, the causative agent of ciguatera fish poisoning (CFP). Ciguatera is the most common foodborne illness related to finfish consumption (Friedman et al., 2017), with estimates of up to 500,000 poisonings per year (Fleming et al., 1998) in tropical and subtropical regions. *Gambierdiscus* dinoflagellates are well-known from coral reef areas, where they are found primarily on the surface of macroalgae. They are consumed by herbivores and detritivores, and the toxins they produce persist through successive trophic levels, eventually contaminating large, mobile, predatory finfish species that are targeted in many recreational and commercial fisheries. Economic impacts associated with ciguatera, ranging from loss of fishing revenue to morbidity from illness, can be considerable; the annual impact of ciguatera in the U.S. was estimated to be in excess of $20 million (Anderson et al., 2000).

While several island regions of the U.S. and its territories (Puerto Rico, the U.S. Virgin Islands, Hawaii) are considered to be hyperendemic for ciguatera, the only ciguatera-endemic mainland region is the Florida coast (Lehane and Lewis, 2000). In contrast, the nGoM has been considered to be at low or unknown risk for ciguatera (Lewis, 2001) because it comprises mainly soft sediment benthos that is not hospitable for *Gambierdiscus* spp. and water temperatures that are thought to be too low for vigorous growth (Kibler et al., 2017). In addition to the ongoing proliferation of artificial hard substrate, there has also been a steady increase in sea surface temperatures over the past decades (Muller-Karger et al., 2015). Villareal et al. (2007) reported the first findings of *Gambierdiscus* spp. in the northern GoM, from six oil platforms and also on floating *Sargassum* seaweed. The authors also hypothesized that the increase in artificial structure in the GoM would facilitate colonization of the area by *Gambierdiscus* spp., thereby aiding range expansion as sea surface temperatures warmed.

Since that first record in the nGoM, diverse *Gambierdiscus* communities have been reported within the FGBNMS in the nGoM (Tester et al., 2013). Five of the seven species known from the Caribbean were found at the east and west Banks, at depths > 45 m, and the authors estimate that conditions at the FGBNMS would provide 200 days of optimal growth conditions annually. The diversity and widespread distribution across the Banks suggests that these communities are able to persist throughout the year. Sea surface temperatures are predicted to continue increasing in the region (Moore et al., 2008), which would increase the number of optimal growing days for *Gambierdiscus* spp. in the nGoM (Tester et al., 2013), and therefore the risk for ciguatera (Tester et al., 2010; Gingold et al., 2014). Another risk factor is range expansion due to warmer waters. As sea surface temperatures increase, *Gambierdiscus* species distributions may shift northward (Hallegraeff, 2010; Parsons et al., 2012), facilitated by the presence of artificial structures in the GoM, which can act as 'stepping stones' for expansion.

Ciguatera cases are routinely reported from the nGOM region. A review of case reports and surveys in Florida estimated the annual incidence at 5.6 cases per 100,000 population, although the incidence rates are higher for the counties in which it is most common (Radke et al., 2015). Export of fish means that ciguatera cases are not always restricted to the source area (CDC, 2009). In the northern GoM, ciguatera cases were reported in 1998 from fish caught off of an oil platform in the region (CDC, 2006) and in 2007 from a gag grouper caught at the FGBNMS (FGBNMS, 2019). The 2007 event was one cause for the FDA to issue a 2008 ciguatera toxin alert for fish caught in the nGoM near the FGBNMS. This later resulted in an industry guidance document for seafood processors, cautioning them about purchasing reef fish caught in areas that were considered to be at risk for ciguatera, including the GoM and the FGBNMS specifically (U.S FDA, 2013). This guidance remains in effect today.

It is clear that the causative agents of ciguatera, *Gambierdiscus* spp., are present throughout the GoM, and that they become sufficiently abundant, at least periodically, to result in toxic fish and human poisonings. Predictions of future risk are difficult because we have so little information on *Gambierdiscus* spp. in the nGoM, which harbors the greatest density of artificial structures. *Gambierdiscus* dinoflagellates occur in multispecies assemblages, and the level of toxicity varies between species (Pisapia et al., 2017), thus both community composition and relative abundance affect ciguatera risk. However, there have been no quantitative measures of *Gambierdiscus* species diversity and abundance from the GoM. We also do not know whether nGoM populations are long-term residents or recent immigrants, and if they are locally sustaining or depend on dispersal from hydrographically connected regions. Populations of *Gambierdiscus* spp. in the US Virgin Islands and the Florida Keys show significant genetic differentiation (Sassenhagen et al., 2018), which suggests that *Gambierdiscus* spp. populations may be fairly isolated. To understand the likelihood and consequences of range expansion in the region, we need to understand the current community composition and distribution within the GoM, the occurrence and routes of dispersal, and the connectivity of nGoM populations to other 'pockets' of *Gambierdiscus* spp. in the Gulf and Caribbean.

FISHERIES ENHANCEMENT

The primary argument in favor of artificial reefs is the enhancement of fisheries, including the recovery of overfished populations (Pickering and Whitmarsh, 1997; Shipp and Bortone, 2009; Bull and Love, 2019). There are two competing hypotheses about the role of artificial reefs for fish stocks (Bohnsack and Sutherland, 1985; Bohnsack, 1989; Pickering and Whitmarsh, 1997): the production hypothesis states that artificial structures increase fish stocks in an ecosystem by providing additional shelter and food, while the attraction hypothesis posits that artificial structures attract fish from nearby areas by providing shelter and food, thus only leading to a redistribution of the existing fish stock.

The red snapper (*Lutjanus campechanus*) fishery, dating back to the mid 1800s, is one of the most important in the GoM, and its history has been reviewed in several recent publications (Shipp and Bortone, 2009; Cowan et al., 2011; Bull and Love, 2019). Other commonly fished species associated with artificial reefs in the nGoM are gray snapper (a.k.a. mangrove snapper, *Lutjanus griseus*, Fischer et al., 2005); vermillion snapper (*Rhomboplites aurorubens*; Allman, 2007), red grouper (*Epinephelus morio,* Bull and Kendall, 1994), greater amberjack (*Seriola dumerilii,* Stanley and Wilson, 1989) and gray triggerfish (Herbig and Szedlmayer, 2016). Artificial reefs are often cited as the primary reason for the recovery of red snapper stocks after the collapse of the commercial fishery in the 1980s (e.g., Shipp and Bortone, 2009), but this notion has repeatedly been called into question. Stanley and Wilson (2000) estimated that artificial reefs have increased the available snapper habitat in the nGoM by only 4.1%, and (Cowan et al., 2011) argued that the recovery only commenced recently, although artificial reefs have existed for decades prior.

When evaluating the impact of artificial reefs on fish populations in the nGoM, the type of reef, location, density, depth and vicinity to other natural and artificial reefs are important factors to consider. There is evidence (Ajemian et al., 2015) that standing platforms support the highest species richness. In this context, a platform depth of around 50 m has been reported to be the most conducive to enhancing fish stocks (Ajemian et al., 2015), likely because this depth represents a transition between coastal and offshore zones. However, there is also evidence of a negative correlation between fish biomass and reef density (Strelcheck et al., 2005). Fish population surveys conducted at HI-389A, a recently reefed platform near the east FGB, found significant overlap in fish community composition between the natural and artificial reefs, but species richness on the artificial structure remained lower than on the natural reef, despite their geographic vicinity (Rooker et al., 1997). Similarly, new artificial reefs deployed near existing natural habitats housed fewer juvenile red snapper than those deployed at larger distances (Mudrak and Szedlmayer, 2012).

These findings show that there is evidence for both production and attraction of fish to artificial structures. Which process dominates can greatly vary temporally and spatially. Broughton (2012) argues that rather than focusing on the dichotomy between production and attraction, a broader evaluation of the ecosystem function of artificial structures and their wide-ranging effects on fisheries is necessary (see Research Priority 3); but there is little doubt that artificial structures have become important components of fisheries species demographies in the GoM.

FUTURE RESEARCH PRIORITIES AND CONCLUSION

We have reviewed the current literature on the roles of artificial reefs in the nGoM in facilitating the establishment of non-native species, promoting population increases of previously habitat-limited species, and their impact on fisheries. There are still large gaps in our understanding of the organismal communities inhabiting the artificial structures that are a prominent part of the nGoM ecosystem, and their interactions with established natural communities like those at the FGBNMS. Based on our review, we have identified three research priorities aimed at improving our understanding of the community ecology of artificial reefs in the nGoM (**Table 1**). For each, we outline potential research approaches, with an emphasis on novel techniques that can be used to provide insight to long-standing questions.

Priority 1

Understand the taxonomic composition of communities on both artificial and natural reefs and how it varies in space and time.

Rationale

We have summarized the evidence for the invasion of some species, but other invasives may have gone unnoticed, as thorough taxonomic surveys have been and continue to be rare. Repeated and continual sampling is critical for detecting new invasions and expansions of existing ones, as well as the appearance of native taxa at new sites. This is especially important for taxa of public health and economic concern, such as jellyfish (see section "Implications of Oil and Gas Structures for Jellyfish Blooms") and *Gambierdiscus* spp. dinoflagellates (see section "Occurrence of Ciguatera Toxin-Producing Dinoflagellates"). Systematic spatial sampling will help us to understand how structure density and proximity to different habitat types may influence community composition, population density, and

TABLE 1 | Proposed research priorities for artificial reefs in the nGoM, methods to address the priorities and their prospective outcomes.

Research priority	Methods	Outcomes
Priority 1: Understand the taxonomic composition of communities on both artificial and natural reefs and how it varies in space and time	Traditional taxonomy	Improve diversity estimates of fouling communities; establish identification guides
	DNA barcoding	Improve taxonomic resolution; establish reference databases for native, non-native species and potentially harmful species (e.g., jellyfish polyps; *Gambierdiscus* spp. dinoflagellates)
	Metabarcoding/metagenomics	Improve efficiency of diversity estimates without the need for labor-intensive traditional taxonomy
	eDNA	Detect presence of species from seawater samples without the need to sample the organism itself.
	Settlement plates (e.g., ARMS)	Improve diversity estimates of fouling communities; observe community succession
	Regular, high resolution sampling of organismal communities on artificial and natural reefs	Improve diversity estimates of fouling communities; detect population increases in potentially harmful species (e.g., jellyfish polyps; *Gambierdiscus* spp. dinoflagellates)
Priority 2: Understand the connectivity of and interactions between natural and artificial reefs	Biophysical modeling combined with high resolution physical oceanography	Describe resilience of reef metapopulations of the nGoM; Identify potential for habitat expansions; Identify high-risk areas for species invasions
	Frequent monitoring of artificial and natural reefs via SCUBA, ROV or other visual surveys, with emphasis on high-risk areas	Early detection of non-native species
	Population genetics/genomics	Model population connectivity, Tracking of origins and invasion pathways of non-native species
	Otolith microchemistry (see also Priority 3)	Assessment of site fidelity to nursery grounds
Priority 3: Multi-year monitoring of fish populations on artificial and natural reefs, including survival and recruitment rates and movement patterns	Reef fish visual censuses (RVC)	Estimates of diversity and abundance of fish on natural and artificial reefs
	Hydroacoustic and video surveys	Fast and non-destructive estimates of habitat use
	Multibeam sonars	Detection and delimitation of large fish aggregations
	Stereo video surveys	Improved accuracy of size estimates; classification of ontogenetic stages
	Otolith microchemistry	Assessment of site fidelity to nursery grounds
	Otolith structural analysis	Aging of fish
	Population genetics/genomics (see also Priority 2)	Model population connectivity

ecosystem function, as well as their potential as stepping stones for habitat expansion.

Research Approaches

Although time and labor-intensive, traditional taxonomy remains an important tool for the characterization of organismal communities. Standardized identification guides are a prerequisite to accurately detect changes in community composition and assess their downstream effects. In addition to traditional taxonomy, genetic and genomic methods are becoming more cost and time efficient as technology advances, and they are particularly useful for the detection of microscopic or cryptic taxa and life stages. They allow the taxonomic identification of individual organisms (DNA barcoding) (Hebert et al., 2003; Miller, 2007) as well as the analysis of community composition (metabarcoding or metagenomics). Environmental DNA (eDNA) from seawater can provide broad coverage of community membership that circumvents the limits of discrete sampling of organisms from substrate (Thomsen et al., 2012). Sampling can also be standardized by deployment of settlement plates. An excellent example of this is the Autonomous Reef Monitoring Systems (ARMS), simple stacks of PVC plates built using a standardized design. Settling organisms are processed using standardized procedures, allowing for direct comparisons between different habitat types or geographic regions (Leray and Knowlton, 2015). If multiple ARMS are deployed on the same structure for different lengths of time, they can also be used to study community succession. In addition, the ARMS provide information on the potential for invasions. Taxa that have dispersed to the area but would otherwise be unable to settle in the adjacent occupied habitat could colonize the ARMS, thus providing information on migration and dispersal. These same samples could be utilized as described in Priority 2 to examine connectivity across the region. Regular monitoring of natural reefs, with emphasis on predicted high risk areas and with increased vigilance after disturbance events such as the sudden mortality event in the East Flower Garden Banks in 2016 (Johnston et al., 2019) may help mitigate any negative effects, e.g., by active removal of invasive species.

Priority 2

Understand the connectivity of and interactions between natural and artificial reefs.

Rationale

Although the debate is still ongoing, there is increasing evidence that artificial reefs can act as stepping stones to facilitate species invasions and range expansions into the nGoM. Non-native and invasive species may negatively affect the health and resiliency of the natural reef communities. Further, the linkages between natural and artificial habitats are not clear – do they act as source or sink? Do artificial habitats promote or reduce genetic diversity within metapopulations? Do they provide trophic subsidies? This is important knowledge for not just introduced or non-native species, but also for indigenous taxa.

Research Approaches

The composition of natural and artificial reef communities is a crucial determinant of their ecosystem function. Understanding the connections between and within these two habitat types is essential for understanding how the current ecosystem state developed, and how it may change in response to disturbance. Biophysical modeling can be used to assess the likelihood of non-native species colonizing natural reefs from nearby artificial structures and to identify high risk focus areas for increased monitoring. In conjunction with high-resolution physical oceanography, biophysical modeling has become an important tool in the estimation of larval dispersal and connectivity in the ocean (Kool et al., 2012), and is especially useful when assessing the metapopulation effects of habitat expansion or removal (Henry et al., 2018), or for designing protected areas (White et al., 2014; Chollett et al., 2017). Biophysical dispersal models can be especially powerful when coupled with population genetics/genomics studies (e.g., Lee et al., 2013; Baltazar-Soares et al., 2018). Population genetic methods can reveal the extent of connectivity or isolation between habitats, provide insight into the source and history of a population, and even assess the extent and direction of migration between sites. Coupled biophysical-genetic models have been applied to habitats on the continental shelf of the nGoM (Garavelli et al., 2018; Studivan and Voss, 2018) but need to be extended to include more taxa with varied life histories.

Priority 3

Examine the broader role of artificial habitats in fisheries, past attraction and production, including more accurate estimates of survival and recruitment rates and movement patterns.

Rationale

The processes of attraction and production of fish to artificial reefs can vary greatly temporally and spatially. Rather than focusing on the attraction/production dichotomy, multi-year monitoring of fish populations on artificial and natural reefs can generate a more nuanced view of the role of artificial reefs for overall ecosystem health and fisheries.

Research Approaches

Continuation of the Reef Fish Visual Censuses (RVC) (Bohnsack and Bannerot, 1986) conducted in the nGoM (e.g., Rooker et al., 1997; Hickerson et al., 2012) would be beneficial to continue monitoring the fish populations, but these methods are expensive (both in time and cost). Otolith microchemistry can be used to determine nursery areas of fish and thus track site fidelity (Patterson et al., 1998; Zapp Sluis et al., 2012). Otolith structural analysis is well-established to age fish, including red snapper (Bortone and Hollingsworth, 1980; Patterson et al., 2001; Wilson and Nieland, 2001). Combining hydroacoustic and video technologies hold great promise for fast and non-destructive surveys of fish populations to identify and monitor habitat use at these sites (Reynolds et al., 2018). Novel stereo video techniques enable more accurate length estimates and allow for improved classification of ontogenetic stages (Davis et al., 2015; Elliott et al., 2017). In addition, the modification and utilization of multibeam sonars provides a new avenue for monitoring and characterizing larger fish populations (Melvin, 2016) although the methods may be limited by depth and adverse weather conditions.

In summary, the nGoM hosts a remarkable diversity of distinct habitats with their associated biological communities, ranging from thriving coral reefs to chemosynthesis-driven cold seep assemblages. Among these diverse habitats, artificial reefs are the newest additions and have led to ongoing 'ocean sprawl' (Duarte et al., 2013; Bishop et al., 2017). While some artificial structures have been in place for about three centuries (Horrell and Borgens, 2014), the majority are active or reefed oil and gas extraction platforms that were deployed over the past 50 years. Other anthropogenic activities, such as shrimp trawling, have long fundamentally altered the GoM ecosystem. It could be argued that the GoM ecosystem has reached a point of no return (Sommer et al., 2019) and the best solution may be to support the services provided by the 'novel ecosystems' of artificial structures (Hobbs et al., 2014) rather than trying to restore the GoM its original condition. Whether we choose to protect the current ecosystem or attempt restoration, it is critical to understand the function of artificial structures.

AUTHOR CONTRIBUTIONS

AS, DE, and MM conceived the idea for this review article. AS wrote the sections "Introduction," "Fouling Communities," "Documented Invasions," "Lionfish," "The Regal Demoiselle, *Neopomacentrus cyanomos,*" "Acorn Barnacles," "Tunicates: *Didemnum perlucidum,*" and "Fisheries Enhancement." MM contributed to the sections "Cup Corals: *Tubastrea* spp.," and "Implications of Oil and Gas Structures for Jellyfish Blooms." DE contributed to the section "Occurrence of Ciguatera Toxin-Producing Dinoflagellates." DH contributed to the section "Connectivity: Stepping Stones, Metapopulations, Resilience, and Replacement." CG provided the figures and contributed the additional text for several sections. All authors contributed to the section "Future Research Priorities and Conclusion," **Table 1**, the final editing, and revisions of the manuscript.

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