SYMPOSIUM

The Effects of Fishing, Climate Change, and Other Anthropogenic Disturbances on Red Grouper and Other Reef Fishes in the Gulf of Mexico

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Synopsis In this article, we consider the potential effects of anthropogenic disturbances on marine fish species known or suspected to be habitat engineers. The three species of interest inhabit different marine habitats at different life stages, and therefore can have significant influences across the sea floor at broad spatial scales. The primary species include the shallow-water Atlantic goliath grouper (Epinephelus itajara), which inhabits mangrove root systems as juveniles, and caves, shipwrecks, and rocky reefs as adults; red grouper (E. morio), which excavates habitat throughout its benthic life in Karst regions of the Gulf of Mexico and western Atlantic, from the coast to the shelf-edge; and tilefish (Lopholatilus chamaeleonticeps), a species that lives on the continental slope and constructs elaborate, pueblo-esque burrows. The anthropogenic disturbances of greatest interest in the Gulf of Mexico include fishing, hypoxia, red tide, oil and gas exploration, and climatic change. We suggest that to understand the broader effects of both natural and anthropogenic disturbances on biomass and productivity in these species requires that we first understand the strength of interactions between them and the other species residing within their communities (e.g., predators, prey, commensals, and mutualists).

Introduction

In 2008, Airoldi et al. opined a limited scientific focus on the repercussions following from loss of structurally complex habitat beyond the consequences to species richness. They pointed out that by ignoring the straightforward feedback loops between homogenization of habitat and diversity at multiple temporal, spatial, and functional scales, in favor of the more expedient species list, we feed the errant fantasy that what we do not know about habitat loss hurts neither us nor habitat. This approach emerges in the primary literature as well as in environmental impact statements (Carney 1996) required by the federal government for oil and gas exploration and development, fisheries, and any other process likely to alter habitat.

Beyond the dearth of information on habitat loss writ large is the somewhat limited range of habitat types explored with sufficient intensity. Coastal sub-tropical and tropical habitats receive more notice and appear to receive the brunt of anthropogenic impacts due to the proximity of humans, while others—especially offshore waters—the shelf, continental margins, slope, and deep-sea regions—are ignored and are assumed to be unaffected. This perception reveals more about our habitat biases (i.e., towards shallow-water tropical and semi-tropical systems such as coral reefs, mangroves, and salt marsh) than it does about vulnerabilities of habitats (Waycott et al. 2009). Continental margins and slopes are highly diverse and dynamic, providing essential ecosystem services throughout the world (Levin and Dayton 2009), with those in the Gulf of Mexico being particularly productive and highly complex (Bouma and Roberts 1990), yet they continue to be used as disposal sites for agricultural and industrial wastes.
In this article, we illustrate habitat connectivity in the Gulf of Mexico through the life cycles of three species that are (or were) important economically to fisheries and ecologically as habitat engineers. We consider the potential impacts that anthropogenic activities such as fishing, pollution, exploration for energy and its development, and climatic change have on them, and the likely synergistic effects of these impacts.

**Connectivity within the Gulf of Mexico**

Two physical processes—circulation patterns and input of freshwater—largely drive productivity and connectivity within the Gulf of Mexico. The Loop Current dominates circulation, entering through the Yucatan Strait, bringing warm Caribbean water onto the West Florida Shelf (WFS), and exiting through the Florida Straits as the Florida Current to feed the Gulf Stream. As it intrudes northward along the WFS, it spins off warm eddies that move to the western Gulf. This combination of features connects remote regions of the shelf horizontally throughout the Gulf of Mexico (Toner et al. 2003; Zavala-Hidalgo et al. 2006) while upwelling associated with the current connects them vertically (Walsh et al. 2009).

Drainage of freshwater into the US Gulf of Mexico includes flow from a number of major river systems and estuaries (Yanez-Arancibia and Day 2004). In the central and eastern US Gulf, the primary influences are the Mississippi River Drainage System, the Western Florida rivers (including the Apalachicola), and discharge of groundwater from dozens of coastal springs (Rosenau et al. 1977; Scott et al. 2004) and from seepage into shallow coastal waters (Taniguchi et al. 2002). Delivery of nutrients from these systems has an influence that varies regionally and seasonally. The Mississippi River delivers agriculturally-derived nutrients that contribute to large-scale hypoxic events each year (Rabalais et al. 2002), while the Apalachicola River delivers a plume of nutrients that fuels productivity during peak spawning of several economically important species of reef fishes (Morey et al. 2009). The Loop Current, then, provides a mechanism for transporting this production, for better or worse, to the western Gulf and along the west coast of Florida to the Atlantic seaboard.

These combined processes contribute to both passive and active transport of materials and organisms among habitats, from architecturally complex foundation-habitats (e.g., salt marsh, sea-grass beds, mangrove forests, oyster reefs) inshore to the continental shelf, slope, and deep sea (Heck et al. 2008) and thus can affect productivity of organisms that have complex life cycles at every life stage. The linkages operate horizontally and vertically across marine strata. Deep-water upwelling brings nutrient-rich waters to the shelf (He and Weisberg 2003) whereas detritus from sea grass moves across the shelf to the deep sea, fueling otherwise nutrient-limited communities (Vetter 1994; Vetter and Dayton 1998). Because these linkages occur over broad temporal and spatial scales, avoiding disruption is critical for maintaining a functional ecosystem.

**The habitat engineers**

The primary species of interest to this discussion include Atlantic goliath grouper (Epinephelus itajara), the largest reef fish in the western hemisphere (up to 3 m and 450 kg); red grouper (E. morio), the most common grouper in the Gulf of Mexico; and tilefish (Lopholatilus chamaeleonticeps), a fishery species about which very little is known. All three are considered to be allogenic engineers (Jones et al. 1994), exhibiting behaviors that transform both the physical and, in all likelihood, the biogenic structure of their habitat. Similarities among these three species include certain life-cycle attributes, behaviors, and associations with habitat. All three species exhibit ontogenetic movements among habitats, from pelagic waters as larvae to widely divergent benthic habitats at different life stages and for the remainder of their lives. The combined effects of living and excavating in one type of benthic habitat during the juvenile stage, carrying out these activities in an alternate habitat as adults, and having generally broad distributions across the continental shelf (Fig. 1) suggest an enormous spatial scale of influence. The fact that all three species are long-lived (35–40 years) also suggests a persistent temporal influence, as well.

Where these species differ, however, is in their distributional patterns, which vary across strata at different depths (Fig. 2). Goliath grouper occurs in shallow (∼35–40 m) tropical and subtropical waters where it is highly sensitive to intrusions of cold (<15°C) water (Sadovy and Eklund 1999). Red grouper occurs across the continental shelf to the edge of the shelf (65–100 m) from tropical through warm temperate waters. Tilefish occur at the continental margin and upper slope (150–500 m) existing within a very narrow range of temperatures (from 9°C to 14°C).
The duration of the pelagic larval stage for the groupers is 4–9 weeks, and is followed by a long-lasting juvenile stage in shallow water, 5–6 years in mangrove habitat for goliath grouper (Koenig et al. 2007) and 4–5 years over inshore hard bottom for red grouper (Coleman et al. 2010). Offshore migrations with approaching maturity land goliath grouper on shallow reefs and red grouper in deeper water nearer the edge of the shelf (Table 1). In contrast, juvenile tilefish occur on the outer edge of the continental shelf and adults on the upper continental slope. Few data on its life history exist, outside of some papers focused primarily on habitat (Able et al. 1982; Grimes et al. 1982, 1985, 1986, 1988; Katz et al. 1983; Grossman et al. 1985; Matlock et al. 1991). Despite its importance as a fishery species, there is little published information about the status of its populations in the Gulf of Mexico (Table 2). An assessment of the stock currently being conducted by NOAA Fisheries (SEDAR...
The three species differ in a number of respects in the way they excavate the substrate. Goliath grouper, which forms the least complex structures, creates relatively shallow “wallows” (Felix-Hackradt and Hackradt 2008; Walter Stearns, Editor in Chief, The Underwater Journal, http://www.underwaterjournal.com/, personal communication; our personal observation). The excavations of red grouper and tilefish are more complex and likely are constructed over a lifetime (Twichell et al. 1985) and across generations (Coleman et al. 2010). As juveniles, red grouper excavate sediment-filled solution holes in bays and shallow coastal areas, some of which appear to be interconnected (Coleman et al. 2010). As adults, they excavate sandy substrata, exposing carbonate rocks and sediment-smothered ledges. Densities of burrows approach 250 km$^{-2}$. Tilefish burrows, excavated in soft (clay) sediments, have been compared to the structures built by Pueblo Indians in the hillsides of Arizona and New Mexico (Grimes et al. 1986). Burrow density is $\approx 600$ km$^{-2}$.

The manner in which these species influence biological diversity is known only at a rudimentary ($\alpha$-level survey) scale for red grouper and tilefish (Jones et al. 1989; Coleman et al. 2010), and not at all for goliath grouper. Excavations harbor other fishery species [e.g., black grouper (Mycteroperca bonaci) and spiny lobster (Panulirus argus) inshore, and juvenile vermilion snapper (Rhomboplites aurolineatum) offshore in red grouper holes; deep-water species, including yellow-edge grouper (E. flavolimbatus) in tilefish excavations], a number of cleaner species, and important prey for the engineers. The fact that this occurs over broad spatial scales suggests that their biogeochemical and ecological influences on the structure and function of communities are neither short-term nor strictly localized.

### Actual and potential anthropogenic impacts in the Gulf of Mexico

#### Effects of fisheries

Fisheries have both direct and indirect impacts on fished species. The most direct impact is the removal of individuals from the population. At low levels of exploitation, removals release the remaining individuals from competition for prey, resulting in faster growth rates as access to food increases. At the other end of the spectrum is a level of removal that first endangers the sustainability of the fishery leading to economic extinction—that is, the population no longer has the capacity to replace itself at the rate that supports fishing—and then threatens or endangers the species’ persistence.

This very simplistic view of a single factor (fishing) driving changes in populations is typical in stock assessments. However, species experience

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<th>Life cycle, habitat, and depth of occurrence of reef-fish architects in the Gulf of Mexico</th>
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<td>Larvae (time)</td>
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<td>Goliath grouper</td>
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<th>Table 2</th>
<th>Population status and conservation status of Atlantic goliath grouper E. itajara, red grouper E. morio, and tilefish Lopholatilus chaemeonticeps in the Gulf of Mexico</th>
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<td>Goliath grouper</td>
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<td>Red grouper</td>
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| Tilefish (golden, sand, blue-line, goldface, black-line, anchor) | Unknown | Unknown | IUCN, International Union for Conservation of Nature; NOAA, National Oceanic and Atmospheric Administration; OF, over fished; OFing, experiencing overfishing.
dynamic trophic interactions that alter productivity and, if the species is keystone, cause cascading trophic effects. The three species evaluated here are nominally considered keystone based on the assumption that the habitat they create is important to the survival of resident species. Severe reductions in the engineer’s populations, then, could translate into equally severe reductions in the distribution of dependent species, with a range of unknown repercussions throughout the system.

Just how vulnerable are these species to fishing? Any large, long-lived species has some measure of vulnerability. Goliath grouper, for instance, is highly vulnerable to exploitation (Sadovy and Eklund 1999) (Fig. 3). It is overfished in the United States (Sadovy and Eklund 1999; NMFS 2009) and critically endangered throughout its range on both sides of the Atlantic (IUCN 2008); the West African population may be extinct (Craig et al. 2009). Despite the protection afforded this species in the United States by a closure of the fishery in 1990, no assessments of populations occurred until 2004 (SEDAR 2004). The lack of baseline data introduced significant uncertainty about the recovery trajectory for this species. Although the fishery remains closed and positive signs of recovery exist (Koenig and Coleman 2009), the species could still be experiencing overfishing from poaching and catch-and-release mortality (Porch et al. 2006) as well as a bottleneck to production caused by poor quality habitat (Koenig et al. 2007). Indeed, anthropogenic alterations of mangrove habitat have impacted structural integrity and are compounded by poor water quality (Koenig et al. 2007), rendering some areas dysfunctional as nurseries for the juveniles’ mandatory 5–6-year sojourn. Populations were further impacted recently by a significant temperature-induced die-off of juveniles (Hallac et al. 2010) that affected multiple cohorts.

Red grouper has a long history of commercial (Schirripa et al. 1999) and recreational exploitation, although the bulk of the catch (≈80–85%) is taken commercially (Schirripa et al. 1999; Coleman et al. 2004b). The commercial fishery operating at outer shelf depths primarily uses bottom long-line gear (GMFMC 2008). Fishers deploying this gear (length 9–42 km, ~125 hooks/km) lay it across the habitat, looping it back and forth to obtain tight coverage of the targeted area, and repeating the practice until the catch diminishes significantly before moving to the next site (J. Nelson, personal communication). The commercial and recreational components focused at inner-shelf depths use vertical hook-and-line gear, the overall effect of which is diffuse, but intense (Coleman et al. 2004a).

Stock-assessment reports (Schirripa and Legault 1999; Schirripa et al. 1999) and updates (SEDAR 2009) have clearly shown the declining status of red grouper (Table 2), with the commercial fishery (primarily long lines) taking about twice as much as the recreational fishery (Fig. 4). There have been significant reductions in biomass, a severely truncated age structure (average age of capture, 7.5 years for a species that lives up to 30 years), and a population hovering just above the overfished condition (Rose and Cowan 2003, SEDAR 2009).

Recent regulatory changes in the red grouper long-line fishery could lead to increased fishing pressure on tilefish and other deep-water species in the Gulf of Mexico. The red grouper fishery was shifted to deeper (>70 m) water to avoid capture of foraging sea turtles after being cited for sea turtle mortalities over 10 times greater than the allowable take (GMFMC 2009). The species affected by this shift include tilefish, snowy grouper (Hyporthodus niveatus), yellow-edge grouper (H. flavolimbatus), speckled hind (E. drummondhayi), and Warsaw grouper (H. nigritus), some of which are designated “species of concern” by NMFS (2009) and considered by the IUCN to be either threatened or endangered (IUCN 2008).

Tilefish are also captured commercially using bottom long-line gear. Although catches in the Gulf of Mexico are much lower than those in the Atlantic (Fig. 5), the density of burrows (600 km⁻²) is much higher. Indeed, in the Atlantic, density of burrows dropped from 258 km⁻² in the late 1970s to 13 km⁻² in the late 1980s, thereby tracking record catches and then declining ones (Barans and Stender 1993) (Fig. 5). This is a strong indication that the long-line fishery, in removing the individual

Fig. 3 Commercial (black line) and recreational (grey line) catch history in metric tons for goliath grouper E. itajara in the Gulf of Mexico (recreational weights converted from number of individuals). Data source Sadovy and Eklund (1999).
fish, contributes to habitat decline as old burrows fall into decay and fewer new burrows are created.

What remains unknown is the indirect effect on species that are associated with the excavations of the habitat engineers. Given that the complexity of the habitat declines demonstrably at high-catch rates (at least for tilefish), presumably the structure of the community is altered over the same spatial scales at which the fishery operates. For tilefish, that means the region from the edge of the shelf down the slope, whereas for red grouper, it means the region between shallow reefs in bays, to the edge of the shelf (Fig. 2). The real effects are hard to determine without experimental no-take zones because there are so few areas that are not fished. By excluding fishing over some defined spatial scale, managers create the opportunity for population recovery that could approach pre-fished levels and thus provide an experimental control for evaluating fishing effects (NRC 2001).

Hypoxia and red tides
Agriculturally released nutrients (primarily nitrogen and phosphate) flowing down the Mississippi and into the northern Gulf of Mexico are notorious for causing large phytoplankton blooms that result in zones of oxygen depletion and significant loss of marine life in the northeastern Gulf of Mexico (Rabalais et al. 2002). Most of the effects occur at relatively shallow (0–60 m) depths, but because of transport and trophic linkages between inshore and offshore waters, loss of productivity inshore has a direct effect on productivity offshore. Although few hypoxic events derived from the Mississippi occur in the eastern Gulf of Mexico, transport of oxygen-depleted water by the Loop Current from the Mississippi Delta to the Atlantic seaboard does occur (Hu et al. 2005).

More common along the WFS at these depths are red-tide blooms, another seasonally occurring nutrient-mediated event in the eastern Gulf of Mexico (Hu et al. 2006) caused primarily by the toxic phytoplankton Karenia brevis (Heil and Steidinger 2009). Both goliath grouper (NMFS 2006) and red grouper (Smith 1975) are susceptible to red-tide blooms. In fact, scientists assessing fishery stocks attribute a recent dip in the biomass of red grouper to an uncharacteristically persistent (year-long) and large (67,500 km$^2$) red tide in 2005 (SEDAR 2009) that also caused a significant die-off of benthic communities, sea turtles, birds, and marine mammals. Hu et al. (2006) suggested a linkage between this event and the inordinately high run-off and ground-water discharge caused by two active hurricane seasons (2004, 2005), with ground-water presenting the highest nutrient source for the bloom.

Despite the characteristically near-shore occurrence of red-tide blooms, dumping of wastes offshore could provide point sources of nutrient delivery to produce offshore blooms at essentially any depth. We mention this not because of any demonstrated connection to the engineering species, but because of the example this provides of using the offshore waters for waste disposal and the susceptibility of these species to harmful algal blooms. In 2003, for instance, the Florida Department of Environmental Protection released >500 million gallons of nitrogen-rich phosphate waste from a defunct South Florida phosphate plant over surface waters on the WFS. The releases occurred over a 5-month period between 46 and 120 miles offshore over 680,000 hectares at depths >200 m. This occurred in the pathway of the Loop Current so that dispersal would be rapid (Hu and Muller-Karger 2003a, 2003b). The waste was treated to reduce nitrogen levels from 600–700 to 15–20 mg l$^{-1}$ (FLDEP 2003) but even this level far exceeded that known to support a red-tide bloom (0.045 mg l$^{-1}$) (Heil and Steidinger 2009). No resultant harmful

Fig. 4 Commercial (black line) and recreational (grey line) catch history in metric tons for red grouper E. morio in the Gulf of Mexico. Data source, NOAA Fisheries.

Fig. 5 Commercial catch history in metric tons for tilefish (Lopholatilus chaemionticeps) from the Gulf of Mexico (black line) and western Atlantic (grey line). Data source, NOAA Fisheries.
algal bloom appeared in surface waters, based on satellite monitoring (Hu and Muller-Karger 2003a, 2003b), but whether or not one occurred at greater depths is unknown because of the limitations of this monitoring technique (Heil and Steidinger 2009); the immediate and cumulative effects remain unknown.

Exploration for energy and its development
Rather than review the litany of ecological impacts of oil spills on marine habitat already amply covered elsewhere (Sanders et al. 1980; Teal and Howarth 1984; NRC 2003) or discuss the possible endpoint of the recent Deep-water Horizon oil spill in the Gulf of Mexico (http://oilspill.fsu.edu), we simply point out two things: (1) that the Loop Current provides an extraordinary mechanism for distributing oil throughout the Gulf of Mexico—to the eastern Gulf by the Loop Current, to the western Gulf by eddies that spin off from the Loop Current, and to the Atlantic Coast as the Loop Current feeds through the Florida Straits to the Gulf Stream; and (2) that the combined effects of oil alone and oil in concert with dispersants (NRC 2005) has the capacity to affect every life stage of the three fish species discussed here—either directly by distribution throughout their habitat or indirectly through trophic interactions. We discuss only two related impacts relevant to ecosystem engineers in the Gulf of Mexico: the effects of exploration with seismic air guns and the impact of laying pipeline on the seafloor. These are important considerations in the eastern Gulf of Mexico because at both federal and state legislative levels, disbanding a moratorium on exploration for oil and gas and its development is under consideration.

Seismic air guns
Arrays of seismic air guns are used in the oil and gas industry to examine geological features down to thousands of meters below the surface for the presence and extent of hydrocarbon reserves. The guns produce high-energy (10–120 Hz) pulses directed downward at intervals of 10–15 s for variable periods of time (even up to a year), and the reflected sound is picked up by hydrophone receivers. In addition to the pulses directed downward there are horizontally directed, low-amplitude, high-frequency sounds up to ~100 kHz that radiate over thousands of kilometers from the source (DeRuiter et al. 2006).

Most research on the sonic impact of seismic air guns focuses on marine mammals, particularly cetaceans (Jochens et al. 2008), whereas considerably less information is available for marine fish. In fact, there are no data on the impact on fishes in the Gulf of Mexico. However, evidence from other species suggests that prolonged exposure to seismic pulses can lower fishery yields by two routes: one, by compromising survival of eggs and larvae (Holliday et al. 1987), and another by disrupting normal distribution and abundance patterns (Hirst and Rodhouse 2000). For example, Engås et al. (1996) found that seismic exploration in the Barents Sea affected catch rates of cod (Gadus morhua) and haddock (Melanogrammus aeglefinus) in the trawl and long-line fisheries. While reductions were obvious 18 nm from the exploration site over a 1600 nm² area, the most pronounced (70%) reductions occurred within the shooting area (30 nm²), with larger fish (>60 cm) being affected more than smaller fish. Abundance, catch rates, and size of fish remained at low levels for the duration of the seismic activity and showed little evidence of recovery after the activity ceased—none at all for haddock in either fishery, or for cod caught in trawls, while there was limited recovery of cod in the long-line fishery. These conditions persisted throughout the 5-day post-shooting period of the study. How long the effects persisted beyond that is unknown.

Seismic blasts could also compromise hearing in fishes (McCauley et al. 2003; Popper and Hastings 2009). McCauley et al. (2003) found that porgy (Pagrus auratus) held in cages and exposed to sounds of air guns suffered extensive damage to the sensory hair cells of the ear. Although not evaluated in fishes (Hastings and Popper 2005), damage to hair cells could translate into permanent loss of hearing. This is more likely to occur in fishes whose alarm response is to retreat to excavations, like the engineers of interest here (our personal observation) than it is in migratory or schooling species like cod and haddock, which tend to disperse. [The tendency to retreat to excavations in the face of disturbances could explain why red grouper appear to be more susceptible to red tide than other species; see Smith (1975, 1976).]

There is an additional concern about the effects of seismic pulses from air guns that relates to sound production in fishes. Both goliath grouper (Mann et al. 2009) and red grouper (D. Mann and M. Montie, unpublished data; our unpublished data) produce sounds during territorial and courtship displays that occur within the same energy range (59–300 Hz) as seismic pulses from air guns. The potential for air guns’ pulses to mask normal intra-specific and inter-specific communications and disrupt important social interactions during critical life stages over large spatial scales is clear and needs evaluation.
Deployment of pipelines
The movement of oil or gas from offshore platforms to inshore sites requires considerable lengths of pipeline to connect the two, 437 nm in the case of the pipeline running between Mobile, AL (USA) and Tampa, FL (USA) to deliver natural gas to Florida (Fig. 6). Pipeline is deployed by a laying barge (~200 m) that systematically lifts and replaces a series of twelve 13-ton (5 × 6 m) anchors on the seafloor as it moves along a transect. As the vessel ratchets forward, it makes two anchor strikes per mile, laying ~1300 m of pipeline each day (each 13-m section of which weighs ~15 tons). Each anchor is attached to the vessel by a steel cable, NM × 7.6 cm in diameter, some portion of which sweeps across the seafloor like a trawl as the vessel moves forward, thereby adding to the damage caused by anchor strikes.

The Mobile-to-Tampa pipeline was placed on the seabed at depths ranging from 244 to 61 m and was buried at water depths shallower than 61 m (Gulfstream 2000). This meant that it crossed the continental slope, ran along the continental shelf margin, and across the shelf’s edge to the Florida coast. The pre-impact surveys evaluated habitat only at depths shallower than 100 m, based on a stipulation by the Minerals Management Service. Thus, there were no surveys of essential habitat for any deep-water fisheries species (including tilefish and a suite of species whose population viability is of concern to both NOAA and the IUCN), or for any deep-water coral-sponge communities. Should the eastern Gulf experience the level of pipeline deployment apparent in the western Gulf (Fig. 6), one could anticipate destruction of a considerable amount of habitat, accompanied by significant changes in biological productivity and diversity as one type of habitat is replaced with another. While some would argue that these activities provide a net increase in habitat, we argue that there is a certain risk in assuming that all habitats are equal in terms of overall productivity and the ecosystem services they provide. This is an important consideration in the eastern Gulf of Mexico, which has some of the most productive fisheries in the United States.

Climatic change
Climatic change operates at so many different organizational levels and scales that it is difficult to predict its consequences for ecological communities (Helmuth et al. 2005; Wiens and Bachelet 2010). The most likely effect on habitat engineers in the coastal zone will result from rises in sea level overcoming biogenic foundation species (=autogenic ecosystem engineers) that provide critical habitat for a suite of economically important species, including other ecosystem engineers (e.g., goliath grouper). While some foundation species could keep pace by migrating landward—e.g., to mangroves (Alongi 2002, 2008; Sanders et al. 2008), salt marshes (Simas et al. 2001; Berry et al. 2002), and oyster reefs (Wright et al. 2005)—this depends on water rising at a sufficiently slow rate to allow this to occur (Gilman et al. 2008). The scenarios may differ in some respects, but most of these habitats have already suffered significant losses for a variety of reasons, among them coastal agricultural, industrial, and urban development (Alongi 1990; Mendelsohn and Mckee 2000; Valiela et al. 2001; Alongi 2002; Waycott et al. 2009), creating a bottleneck to productivity in some cases (Koenig et al. 2007). The impact of a rise in sea level could remove what remains (Nicholls et al. 1999; Bell 2008).

Rising water temperatures are likely to have a variety of physical effects on the patterns of circulation (Kennett and Ingram 1995), including the Loop Current, and on the intensity of upwelling (Barth et al. 2007) that result in compromised mechanisms of transport of nutrients and larvae (Sponaugle et al. 2007), and lead to shuffled communities as species expand their distributions into novel habitats (Hoegh-Guldberg 1999; Sagarin et al. 1999, Schiel et al. 2004). Shifts in larval distributional patterns are problematic for our species of interest, all of which have larvae with long (40–60 days) pelagic stages. Although the actual transport mechanism of larvae during this stage is unknown—although it likely includes the combined effects of passive transport and active swimming—they could be transported away from highly productive habitats if the current patterns are altered, ultimately resulting in poor recruitment. Tilefish, with its limited

![Fig. 6 Pipelines in the US waters of the eastern Gulf of Mexico. Data source, Minerals Management Service.](https://academic.oup.com/icb/article-abstract/50/2/201/613731/613731)
temperature range, would likely experience compression of its distribution.

**Conclusion**

The habitat engineers examined here demonstrate the complex vertical (benthic-pelagic coupling) and horizontal (inshore to offshore) linkages that exist among habitats, species, and marine strata at multiple spatial and temporal scales. They are linked physically through oceanic currents and biologically through ontogenetic migrations and trophic interactions.

The next step is to expand the focus from alpha-level surveys of the patterns of biodiversity associated with ecosystem engineers to evaluating strengths of interactions among those species associated with engineers over broad spatial and temporal scales, including predators, prey, commensals, and mutualists. Also important is the influence that their interactions have on ecosystem services at a “functional” level. Tests for the strength of interactions include direct approaches, e.g., field experiments (Paine 1992), laboratory experiments (Abrams 2001), observations (Wootton 1997), or analyses of system dynamics (Laska and Wootton 1998), indirect approaches (e.g., using relative allometric measures among species (Emmerson and Raffaelli 2004; Sala and Graham 2002), “interaction strength-free” approaches (estimating community response to environmental perturbations (Wootton 2005)], or some combination of these (O’Gorman et al. 2010). Regardless of the approach, the overwhelmingly consistent result is that there are far more weak interactions than there are strong ones (Paine 1992), and that their predominance has an overriding influence on maintaining community resilience. Teasing out the significant interactions among species in a complex system is a difficult but necessary task if we are to understand the consequences of both natural and anthropogenic disturbances (Wootton and Emmerson 2005). Only then can we hope to anticipate the tipping points at which profound changes might occur.

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