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Seaweed structure shapes trophic interactions: A case study using a mid-trophic level fish species

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ABSTRACT

Biogenic habitat structure, such as that created by foundation macrophytes, shapes the interactions of higher trophic level organisms by creating three-dimensional refuge spaces. In recent decades, many kelp habitats have transformed into turf-dominated communities. This represents a fundamental change in the overall habitat structure in these communities, with an unknown impact on upper trophic level organisms. We investigated how macroalgae morphology affects a common residential mid-trophic level wrasse, *Tautogolabrus adspersus* (cunner), which utilizes macroalgae for both refuge and foraging. Three studies were conducted: in situ behavioral video observations, a refuge choice experiment, and a foraging efficiency experiment. Video observations revealed that in kelp-dominated and mixed habitat types cunner use macroalgae more often for refuge than for foraging, but in turf-dominated habitats refuge and foraging events were equal. In these habitats, refuge-seeking was more often associated with a tall, morphologically simple kelp. The refuge choice experiment supported our video observations with cunner preferentially seeking refuge beneath taller but less morphologically complex algae instead of shorter filamentous forms. In predation trials, macroalgae complexity did not significantly affect the number of prey the fish captured. Our results provide evidence that the refuge-seeking behavior of this residential mid-trophic level fish may be impacted by the ongoing shifts in macroalgae dominance in the Gulf of Maine. Loss of its preferred refuge (tall, canopy-forming kelps) may force it to use the less-preferred introduced turf algae instead. However, whether turf provides sufficient protection for this species remains unclear. With the ongoing loss of kelp in temperate coastal ecosystems worldwide, it is important to understand the potential indirect effects that changes in habitat structure will have on the trophic interactions of upper level organisms.

1. Introduction

The importance of functional traits over species identity in controlling patterns of community ecology has been shown in recent studies (McGill et al., 2006; Verberk et al., 2013; Webb et al., 2010). The growing area of functional ecological research incorporates features at the individual level and scales them to make predictions of community-level processes (McGill et al., 2006; Violle et al., 2007). Functional traits are quantifiable characteristics of an organism, measured at the individual level but comparable across species (i.e. maximum body size, metabolic rate, canopy height) (McGill et al., 2006). One of the main concepts of trait-based ecology is that patterns and processes at a community or ecosystem level are determined by the characteristics of the component species, not by their taxonomic identity (Griffin et al., 2009; Gross et al., 2017; Jänes et al., 2017). For example, competition among trees was found to be predictable based on the traits of wood density, specific leaf area, and maximum height (Kunstler et al., 2015), while primary production in certain aquatic biomes was determinable based on the morphological, life history, and tolerance traits of marine macrophytes (Jänes et al., 2017).

Habitat structure in a system provides novel microhabitats, mediates predator-prey interactions, and alters the physical environment (Heck and Crowder, 1991; Jones et al., 1994; Crooks, 2002; Grabowski and Powers, 2004). Macrophytes are some of the most important structure-forming organisms in many ecosystems. The morphology and structure of macrophytes has long been recognized as a key regulating component across a diversity of terrestrial, aquatic, and marine ecosystems (Lawton, 1983; McCoy and Bell, 1991). For example, ecological processes are shaped by the physical structure of forest canopies (MacArthur and MacArthur, 1961; Rotenberry and Wiens, 1980), seagrass beds (Orth et al., 1984; Schmidt et al., 2011), and mangroves (Nagelkerken et al., 2008). Bird species diversity has been shown to be

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controlled by the foliage height profile (MacArthur and MacArthur, 1961), while the height and complexity of grass appears to modify the strength of top-down control of various arthropods by spiders (Sanders et al., 2008). In some marine and aquatic systems, more complex macrophytes reduce the ability of predators to locate and consume prey (e.g. Holmlund et al., 1990; Warfe and Barmuta, 2004). Large kelps in temperate marine areas create three-dimensional structure, facilitate understory diversity, and protect against physical disturbances (Teagle et al., 2017). Despite the obvious differences between terrestrial and aquatic habitats, the role of biogenic structure is similar whether in land or water. Three-dimensional structure mediates species interactions by providing visual cover, interstitial refuge spaces, and increasing the overall available surface area in an ecosystem.

Due to the intricate connections between biogenic habitat structure and animal ecology, we may expect that the ability of animals to find suitable refuge and food will be impacted in ecosystems in which dominant foundation species have been lost or replaced by morphologically different species. Over the last few decades, there has been drastic human-mediated change in foundation species (McIntyre et al., 2015; Thomson et al., 2015; Wernberg et al., 2016), with concurrent changes in habitat structure (Coleman and Williams, 2002; Ellison et al., 2005; Asner et al., 2008; Thomson et al., 2015; Dijkstra et al., 2017). Some of these architectural changes are caused by extreme climatic events (Wernberg et al., 2013; Thomson et al., 2015) or by direct human removal of foundation species (Coleman and Williams, 2002; Ellison et al., 2005). Another source of architectural change in ecosystems is the proliferation of invasive species. Biogenic structure-forming introductions typically alter physical habitats either by creating novel structure where none existed previously (i.e. Posey, 1988; Wright et al., 2014), or by replacing a morphologically dissimilar native species (Smith and Finch, 2013; Dijkstra et al., 2017). Morphological differences between native and introduced plants has been shown to impact the availability of various seasonal resident bird nesting sites (Smith and Finch, 2013), foraging success, predator avoidance (Barnes et al., 1995), and other community interactions (see Nelson et al., 2017 for review). Regardless of the source of these macrophyte shifts, the impacts on the trophic interactions of other organisms in these systems are complex and understudied.

In the shallow rocky subtidal of the southern Gulf of Maine, habitat structure has historically been provided by large kelps (Order Laminariales). Species such as *Saccharina latissima* form a relatively tall canopy over a diverse and protected understory (Chapman and Johnson, 1990; Levin et al., 2002; Steneck et al., 2013). However, the Gulf of Maine is one of the fastest warming bodies of water globally (Pershing et al., 2015), and in recent years kelp abundance has begun to decline in this region (Dijkstra et al., 2017; Witman and Lamb, 2018). The benthic community is increasingly dominated by a variety of low-lying turf algae, which are morphologically distinct from the tall flat-bladed kelps, with lower canopy height and increased thallus complexity (Dijkstra et al., 2017). This pattern is similar to that seen in other kelp systems worldwide (Filbee-Dexter and Wernberg, 2018). Mechanistically, increasing thallus complexity may inhibit predation by visual predators such as fish by providing more interstitial refuges for prey (Steneck et al., 2013). A number of the newly dominant turf algae are introduced species, including *Dasysiphonia japonica*, a complex filamentous red alga which has rapidly spread through New England (Schneider, 2010; Ramsay-Newton et al., 2017).

We coupled field and laboratory studies to investigate how these documented changes in the structure of foundation species will affect the trophic interactions of the demersal wrasse *Tautogolabrus adspersus* (cunner). Cunner are an ideal study organism to address questions of habitat change in this ecosystem due to their middle trophic position, behavioral reliance on macroalgae, and their abundance in this system. We predicted that cunner would be sensitive to changes in the architecture of the macroalgal assemblage due to their dual role as both predator and prey in this habitat. We investigated the effect of varying macroalgae morphology on two main aspects of cunner ecology: refuge and foraging. These aspects were tested using three related studies: in situ behavioral observations, a refuge choice experiment, and a foraging efficiency experiment. We expected that cunner would prefer taller, broad-bladed macroalgae such as kelps over low-growing turf algae species for refuge in the field and in the laboratory experiment. We also predicted that cunner foraging efficiency would be reduced within turf algae monocultures due to the small-scale complexity of these algae.

2. Materials and methods

2.1. Study species

Tautoglolabrus adspersus (cunner) was chosen for this study due to its local abundance (Witman and Lamb, 2018), and its middle trophic level. Cunner range along the Atlantic coast of North America from Newfoundland to New Jersey, and are among the most common fish in the rocky subtidal reefs of the Gulf of Maine (Bigelow and Schroeder, 1953; Ojeda and Dearborn, 1991). Most cunner are found < 10 km from shore, in relatively shallow waters (2 to 20 m), where they inhabit eelgrass, kelp beds, boulder fields or dock pilings depending on the location (Bigelow and Schroeder, 1953) Cunner are closely associated with the benthos, and rarely stray far from their home territory. They establish seasonally permanent territories on the seafloor where they seek out invertebrate prey on the substrate or within macroalgae (Chao, 1973; Pottle and Green, 1979; Green et al., 1984).

As opportunistic predators, cunner feed on a variety of small invertebrates, including isopods, amphipods, juvenile urchins and lobsters (Olla et al., 1975; Johns and Mann, 1987; Ojeda and Dearborn, 1991; Bowman et al., 2000). Post-settlement, juvenile cunner are preyed upon by benthic predators such as sculpins and sea robins (Tupper and Boutilier, 1997). Although mature cunner have not been found to make up the bulk of any larger predator's diet, they are still preyed upon by seabirds, seals, and larger predatory fish (Blackwell and Sinclair, 1995; Hall et al., 2000; Hammill and Stenson, 2000; Nelson et al., 2003; Ojeda and Dearborn, 1991). Chao (1973) observed that cunner seek refuge from these predators by hiding under kelp blades.

Cunner typically grows to a maximum length of 15 to 25 cm, although they reach maturity at approximately 6 to 7 cm long at two or three years old (Bigelow and Schroeder, 1953). The fish used in the following laboratory experiments were between 6 and 12 cm on average, probably nearing or just past maturity, and represented the most common size cunner in our study sites.

2.2. Field video observations

To examine how cunner utilize macroalgae structure in situ, stationary video footage was collected from nine subtidal reef sites around coastal Maine and the Isles of Shoals between July and August 2015 and July and August 2016 (Fig. 1). All sites ranged in depth between 8 and 11 m. Sites were classified as being either kelp-dominated, turf-dominated, or mixed based on the results of a 100 m^2 mosaic survey of macroalgal coverage conducted at each site (Table 1). To document fish behavior, a GoPro Hero 3+ camera was deployed at each site using SCUBA. It was attached to a metal frame which suspended it 0.5 m above the seafloor. The camera was positioned to look horizontally out over the habitat, and left to record fish behavior for approximately 1 h (see Witman and Lamb, 2018). All dives were conducted in the morning.

Video footage was later reviewed, and the length of all videos was standardized by using only the first 50 min of footage. All fish and large animals visible in video footage were identified to species if possible, although behavior was only analyzed for cunner. Behavior was quantified by counting the number of times a cunner interacted with macroalgae. Interactions were categorized as either refuge actions (the fish