

## 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, *Tautoglabrus 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 *Tautoglabrus 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

*Tautoglabrus 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).

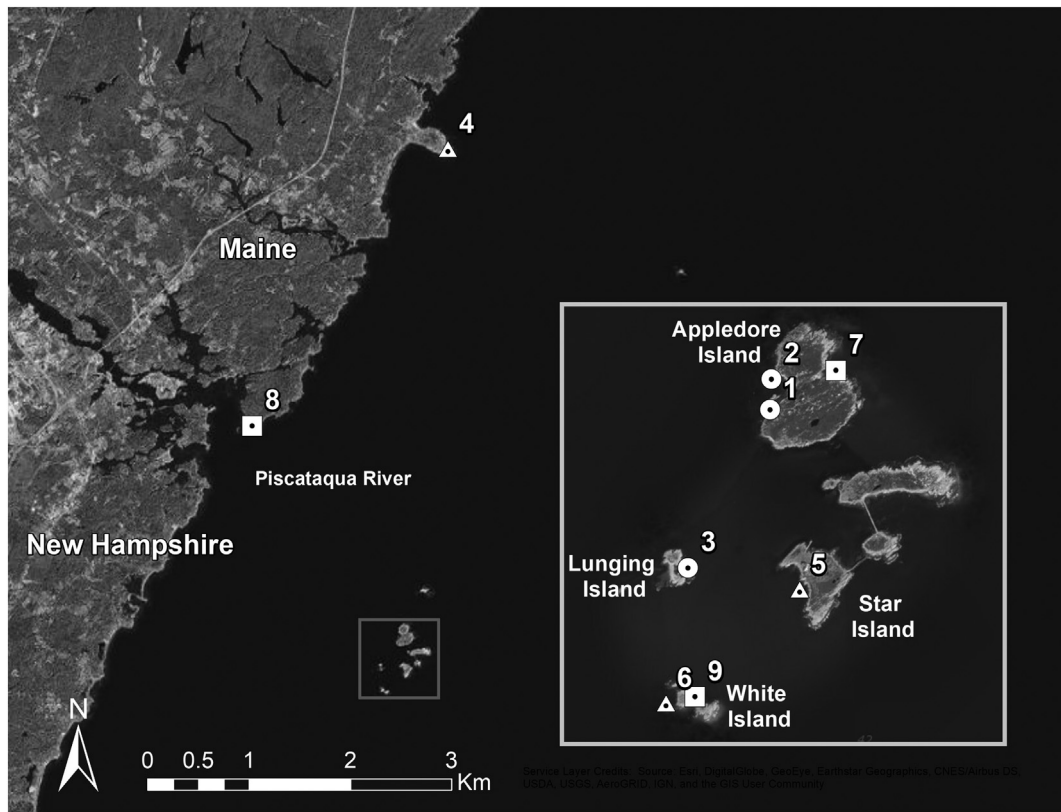
As opportunistic predators, cunner feed on a variety of small invertebrates, including isopods, amphipods, juvenile urchins and lobsters (Olla et al., 1975; Johns and Mann, 1987; Ojeda and Dearborn, 1991; Bowman et al., 2000). Post-settlement, juvenile cunner are preyed upon by benthic predators such as sculpins and sea robins (Tupper and Boutillier, 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<sup>2</sup> 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



**Fig. 1.** Map of video observation locations in coastal Maine and the Isles of Shoals (inset). Dominant habitat type at each site is designated by marker shape: Circles represent kelp-dominated, triangles represent mixed, and squares represent turf-dominated. Sites are: 1. Babbs Cove, Appledore Island; 2. Cribbs, Appledore Island; 3. Lunging Island; 4. Nubble Point, York ME; 5. Star Island; 6. White Island Exposed; 7. Broad Cove, Appledore Island; 8. Fort Foster, Kittery ME; 9. White Island Cove.

swam underneath or in an individual macroalgae for any reason), or foraging actions (obvious darting movement toward the macroalgae associated with attack of a prey item) (see [Tupper and Juanes, 2017](#)). For each interaction event recorded, the associated macroalgae species was noted.

While there were other macroalgae species visible in the videos, we specifically focused on *S. latissima* and *D. japonica* as the vast majority of events involved one of those two macroalgae. For the purposes of analysis, the individual algae were classified as microhabitats. The category “other” for refuge events refers to different macroalgae species, while “other” in feeding events refers to macroalgae species and water column feeding activity.

**2.3. Refuge choice experiment**

To test habitat preferences of young-of-the-year and juvenile cunner, a refuge choice experiment was performed at Shoals Marine

Lab on Appledore Island, Maine between August 1 and August 5, 2014. Trials were conducted to measure the amount of time cunner spent seeking refuge among three morphologically distinct macroalgae in a controlled environment. Fish collection and handling permits were under the auspices of the Shoals Marine Laboratory.

Cunner were collected using baited minnow traps deployed from the lab's dock in Babb's Cove. The fish were kept in a holding tank with flow through seawater, rocks, and sections of PVC pipes for approximately 4 days prior to use in the experiment to allow for acclimation to the laboratory setting.

Three species of macroalgae representing high, medium, and low complexities (see [Dijkstra et al., 2017](#)) were chosen: *D. japonica*, *Dumontia contorta*, and *Ulva lactuca* respectively ([Table 2](#)). Although no kelp species were used for this experiment, *U. lactuca* was chosen as it was a manageable size for our tank studies. Its simple blade-like morphology and greater height compared to *D. japonica* or *D. contorta* makes it reminiscent of the taller but still low complexity *S. latissima*

**Table 1**

Designated habitat type and estimated percent cover of dominant algae at study sites, based on 100 m<sup>2</sup> mosaic survey conducted at each site. *Saccharina latissima* was the most abundant kelp species, while *Dasysiphonia japonica* was the most abundant turf species. Other represents both additional algae species and substrate not colonized by algae.

Site	Location	Habitat type	Percent cover <i>S. latissima</i>	Percent cover <i>D. japonica</i>	Percent cover other
1	Babbs Cove	Kelp-dominated	65	20	15
2	Cribbs	Kelp-dominated	55	38	7
3	Lunging Island	Kelp-dominated	75	20	5
4	Nubble Point	Mixed	30	30	40
5	Star Island	Mixed	45	50	5
6	White Island Exposed	Mixed	35	40	25
7	Broad Cove	Turf-dominated	25	50	25
8	Fort Foster	Turf-dominated	5	40	55
9	White Island Cove	Turf-dominated	25	50	25

**Table 2**

Summary of traits of macroalgae species used in these studies. Fractal dimension (Mean  $\pm$  SE) is a metric of two-dimensional macroalgae complexity. Complexity values adopted from Dijkstra et al., 2017 (exception is *D. contorta*). *D. contorta* was collected from the Isles of Shoals in 2014 and complexity calculated. Height in cm (Mean  $\pm$  SE) taken from macroalgae used in the experiments with *S. latissima* values taken from specimens collected in the field.

Species	Shape	Fractal dimension	Complexity	Height
<i>Chondrus crispus</i>	Foliose	1.14 $\pm$ 0.02	Medium	8.90 $\pm$ 0.41
<i>Codium fragile</i> <i>spp. fragile</i>	Branched	1.10 $\pm$ 0.01	Medium	22.03 $\pm$ 3.20
<i>Dasysiphonia japonica</i>	Filamentous	1.53 $\pm$ 0.03	High	13.73 $\pm$ 0.41
<i>Dumontia contorta</i>	Branched	1.22 $\pm$ 0.02	Medium	7.89 $\pm$ 0.48
<i>Saccharina latissima</i>	Flat	1.05 $\pm$ 0.01	Low	166.22 $\pm$ 19.29
<i>Ulva lactuca</i>	Flat	1.05 $\pm$ 0.03	Low	36.11 $\pm$ 2.58

and thus appropriate for this investigation of functional traits. Height (cm) and biomass (wet weight, g) of individual macroalgae were assessed for each trial. Height of individual macroalgae used in each trial was measured by individuals on a flat surface and measuring from the holdfast to the tip of the algae; wet weight was measured by placing individual in a salad spinner, blotting the specimen dry using a paper towel and then weighing it. Complexity as measured by fractal dimension of individual macroalgae could not be assessed as the algae could not be pressed after spinning. Samples of all three species were collected via SCUBA from shallow subtidal sites near Appledore Island. For each trial, one sample of each macroalgae species was affixed to a small rock with superglue, then placed in the tank according to one of four randomly selected pre-determined arrangements. Any invertebrates still inhabiting the macroalgae following collection were not removed before conducting the trials. Macroalgae samples were replaced for each trial.

Trials ( $n = 20$ ) were conducted in a  $\sim$ 110 L flow through seawater tank. The tank was divided into two equal compartments using fine mesh. This allowed us to conduct two trials simultaneously. A GoPro Hero 3+ was affixed above the experimental tank to film each trial. The tanks were located under a covered deck and as such were covered with chicken wire to prevent predation of fish by gulls. Although fish were protected, the presence of nearby birds seemed to startle them into seeking refuge. For each trial, one cunner was placed into the experimental tank with the three different macroalgae samples. They were left undisturbed and their behavior was recorded for one hour. Video footage from the trials was later analyzed by recording the amount of time the fish spent seeking refuge under any of the three macroalgae specimens.

After the trial was completed, fish were temporarily anesthetized using tricane methanesulfonate (TMS) in order to measure length (cm) and mass (g) with minimal stress to the animals (Carter et al., 2011). Anesthetization involved immersing each fish in a bath of 30 mg/L TMS mixed with seawater and waiting approximately one minute or until the fish exhibited reduced swimming behavior (Carter et al., 2011). After being measured, the fish were returned to fresh seawater and watched until they no longer exhibited signs of anesthesia. Individual cunner was only used for one trial before being measured and released. The mean cunner size used in trials was 6.70 cm (se 0.36) and mean weight was 5.25 g (se 0.73). Fish were released in a different but nearby location, from the collection location to ensure that animals were not being recaptured.

#### 2.4. Foraging experiment

Foraging trials were conducted to test the ability of juvenile cunner

to consume invertebrate prey within monocultures of algae with differing morphologies. Treatments included: *S. latissima*, *Codium fragile* subsp. *fragile*, *Chondrus crispus*, and *D. japonica*, and a control with cunner and amphipods only. The four macroalgae species represent a variety of morphological forms with complexities ranging from low to high (Table 2). Different macroalgae species were used in this study compared to the refuge choice experiment based on algae availability in the field, and due to our interest in morphological complexity (see Dijkstra et al., 2017) over species identity.

Trials were run at the University of New Hampshire's Coastal Marine Lab in New Castle, New Hampshire between September and October 2016. Cunner were collected using baited minnow traps deployed at various sites along coastal New Hampshire and southern Maine (Permit numbers NHFG 1637 and ME 2016-93-00). Cunner were kept in 1 m diameter round tanks with flow through seawater at ambient temperature for at least 24 h prior to use in experimental trials. Isopod prey (*Idotea baltica*) were collected by hand from the waters near the marine lab and kept in a 30 L aquarium with fresh seawater. A representative sample ( $n = 31$ ) of isopods was measured to determine the average length (13.3 mm, SE 0.97) and width (3.8 mm, SE 0.28) of these prey items. Samples were collected by hand using SCUBA from various locations in coastal New Hampshire and southern Maine.

Trials were conducted in  $\sim$ 40 L aquaria tanks filled with seawater at local ambient temperature (mean 14.9 °C, SE 0.124) and equipped with an airstone for oxygenation. Five tanks were set up to run all treatments simultaneously. The sides of each tank were covered with black plastic sheeting to prevent influence from outside stimuli and to allow for independence between trials. For each tank, one of the four macroalgae monoculture treatments was randomly assigned, or a control treatment with no algae. For the algal treatments, five pieces of one species of macroalgae were attached to small rocks and placed haphazardly on the bottom of the tank. For the control treatment, five rocks were haphazardly placed in the tank with no macroalgae attached. Thirty isopods were added to the tank and allowed to acclimate for 1 h. Following the isopod acclimation period, one cunner was added to the tank and allowed to feed for 3 h. Preliminary studies indicated this allowed enough time for the fish to acclimate and feed. At the end of the designated feeding time, fish were removed from tanks and the remaining isopods were counted. Nine replicate trials of each treatment were conducted ( $n = 45$  total). Between trials, water and algae were replaced for each tank.

Cunner were temporarily anesthetized using TMS in order to measure mass (g), length (cm), and gape width (mm) with minimal stress to the animal following the same procedure as described above. Mean cunner mass for the foraging study was 21.67 g (se 2.48), while the mean length was 10.96 cm (se 0.39), and the mean gape width was 5.41 mm (se 0.20). There were no significant differences in cunner mass, size, or gape width among the treatments (ANOVA; mass:  $df = 4$ , 45,  $F = 1.6884$ ,  $p = 0.2001$ ; length:  $df = 4, 45$ ,  $F = 1.48$ ,  $p = 0.2241$ ; gape:  $df = 4, 45$ ,  $F = 1.5646$ ,  $p = 0.2001$ ).

Cunner was then released near their original capture location. Each trial within an individual tank was considered to be an independent replicate. Cunner was only used for one trial to avoid potential biases. The University of New Hampshire's College Animal Care and Use Program (protocol # 160607) approved field collection, sedation and laboratory fish studies.

#### 2.5. Statistical analysis

For field studies, a two-way repeated measures analysis with behavior and habitat as the independent factors, sites nested within habitat as the random effect, and habitatXbehavior as the interaction term was used to examine differences whole proportion refuge and foraging events. On finding a significant difference, post-hoc Tukey HSD test, set to 0.01 significance, was used to assess pairwise differences between treatment means. A subsequent two-way ANOVA with habitat (site

dominated by *S. latissima*, mixed or *D. japonica*) and microhabitat (macroalgal species, e.g., *S. latissima*, *D. japonica* or other) as treatments was used to examine differences in proportion of refuge or foraging events. Variances for raw proportion of time refuge and foraging were homogeneous across habitat types (Levene's test,  $p < 0.05$ ).

A repeated measures analysis with refuge (i.e., individual macroalgae or exposed) use as the repeated variable, trial and compartment nested within trial as a random effect was used to detect differences in proportion of time cunner spent in or close to macroalgal laboratory treatments. To examine whether macroalgae biomass or height had an effect on proportion of time fish spent in a particular macroalgae, a multiple regression was performed.

A mixed model with macroalgae treatment as the fixed factor and trial as the random effect was performed to test for differences in proportion of prey consumed among macroalgae habitats. Simple linear regressions were run to test the relationships between fish mass, length, or gape width and proportion of prey consumed.

Variances for macroalgae treatment in the laboratory studies remained heterogeneous (Levene's test,  $p < 0.05$ ) despite arcsine transformation, so untransformed proportion of time were used in all univariate analyses. Results were evaluated at a conservative significance level of 0.01. On finding a significant difference, post-hoc Tukey HSD test, set to 0.01 significance, was used to assess pairwise differences between treatment means. All statistics were performed using the JMP© 12 statistical software package.

### 3. Results

#### 3.1. Field video observations

A total of 414 refuge and foraging activities were recorded. In addition to cunner, striped bass (*Morone saxatilis*), Pollock (*Pollachius virens*) and harbor seals (*Phoca vitulina*) were seen in the video footage, all of which are known predators of cunner. Cunner displayed  $\sim 3\times$  more refuge events in kelp and mixed habitats (Fig. 2). In turf habitats, cunner foraged and sought refuge equally. Overall, there was a significant effect of behavior with greater refuge than foraging events ( $F_{1,12} = 61$ ,  $p < 0.01$ ). There was no effect of habitat ( $F_{2,12} = 1.65$ ,  $p = 0.27$ ), but a significant interaction effect of behavior and habitat ( $F_{2,12} = 5.70$ ,  $p = 0.04$ ). Within habitats, there was a significant whole model effect on the proportion of refuge events (Fig. 3;  $SS = 3.08$ ,  $F_{8,18} = 26.85$ ,  $p < 0.01$ ). Microhabitats and the interaction between

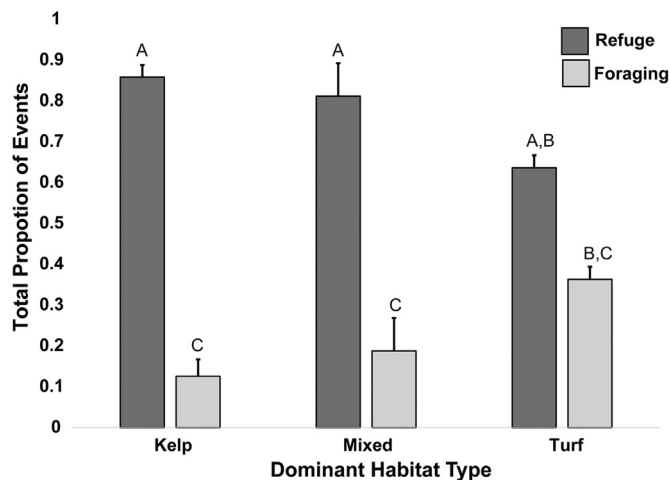


Fig. 2. Total proportion ( $\pm$  SE) of cunner refuge-seeking and foraging events observed *in situ*, by dominant habitat type ( $n = 3$  per habitat). Letters denote statistically significant differences. Cunner displayed more refuge than foraging actions in kelp and mixed habitats and equal foraging and refuge in turf dominated habitats.

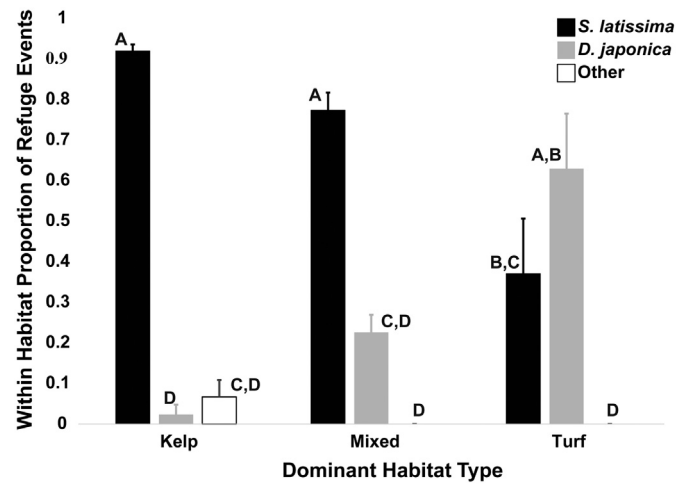


Fig. 3. Within habitat proportion of cunner refuge-seeking events ( $\pm$  SE) grouped by microhabitat ( $n = 3$  per habitat). Letters denote statistically significant differences. Cunner used *Saccharina latissima* for refuge in kelp and mixed habitats and *Dasyphyllia japonica* and *Saccharina latissima* in introduced habitats.

microhabitats and habitats were found to be significant ( $SS = 2.02$ ,  $F_{2,18} = 70.31$ ,  $p < 0.01$ ,  $SS = 1.06$ ,  $F_{4,18} = 18.54$ ,  $p < 0.01$ , respectively). There was no significant effect of habitat on the proportion of refuge events across habitats ( $SS = 0.00$ ,  $F_{2,18} = 0.26$ ,  $p < 0.99$ ). Differences in microhabitat usage (*S. latissima*, *D. japonica* and other) were observed for each habitat type. Within habitats, cunner were found to seek refuge in *S. latissima* more frequently in kelp and mixed habitats and equally in *S. latissima* and *D. japonica* in introduced ones (Tukey HSD,  $p < 0.05$ ). There was no difference of within habitat effect on the proportion of foraging events (Fig. 4;  $SS = 0.52$ ,  $F_{8,18} = 0.99$ ,  $p = 0.47$ ).

#### 3.2. Refuge choice experiment

There were significant differences in the amount of time cunner spent seeking refuge in each of the treatment choices (Fig. 5;  $F_{3,57} = 29.65$ ,  $p < 0.01$ ). Significantly less time was spent around the short, medium complexity *D. contorta* than underneath the taller and morphologically simple *U. lactuca* or in *D. japonica* or exposed (Fig. 5;

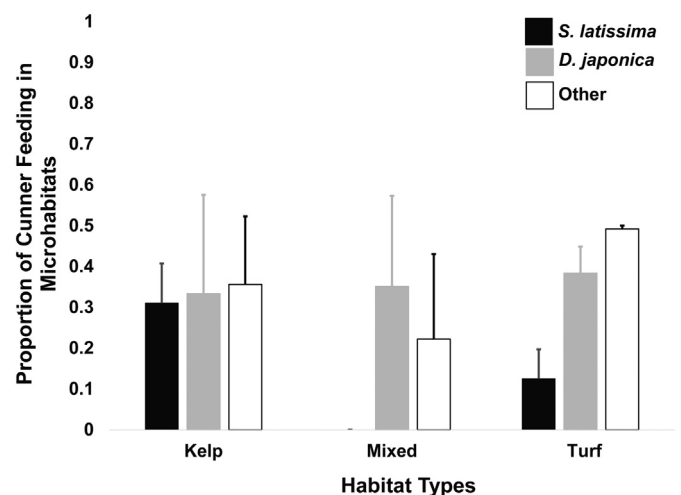


Fig. 4. Within habitat proportion of cunner foraging events ( $\pm$  SE) grouped by microhabitat ( $n = 3$  per habitat; algae species: *S. latissima*, *D. japonica*, or other). There was no significant difference in foraging actions across habitat types or within microhabitats.

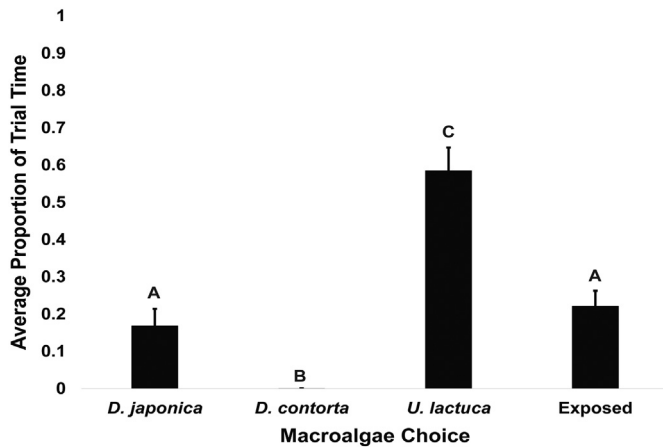


Fig. 5. Mean ( $\pm$  SE) proportion of trial time spent by cunner seeking refuge under either *Dasyisiphonia japonica*, *Dumontia contorta*, or *Ulva lactuca*, or exposed under no cover ( $n = 20$ ). Letters denote statistically significant differences. Cunner spent more time near the taller, less complex *U. lactuca* than in the shorter and more complex *D. japonica* or *D. contorta*.

Tukey HSD set to 0.01 significance). A multiple regression with weight and height as variables indicated that height was the only significant term in the multiple regression for time spent close to a macroalgae with an adjusted  $r^2$  value of 0.51 ( $SS = 1.11$ ,  $F_{2,57} = 31.7$ ,  $p < 0.01$ ; height (mm)  $p < 0.01$ , biomass (g),  $p = 0.35$ ).

### 3.3. Foraging experiment

No significant differences in the proportion of prey consumed was found among treatments (Fig. 6;  $F_{4,32} = 1.93$ ,  $p > .13$ ). The proportion of prey consumed was not significantly correlated to fish length, mass, or gape width (linear regression,  $p > .05$ ).

## 4. Discussion

Our laboratory and field studies indicate the functional traits of height and complexity of macroalgae mediate refuge-seeking and foraging behaviors of cunner. Cunner spent more time seeking refuge in the flat-broad blades of *S. latissima* than feeding, suggesting this morphological type is a critical component of the habitat. Our results, along

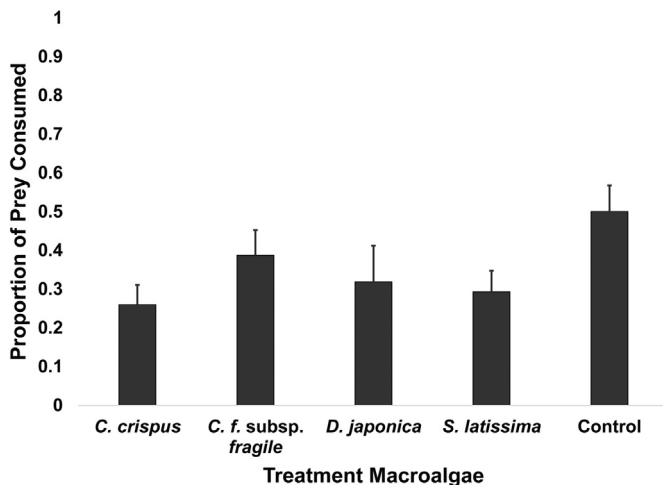


Fig. 6. Mean ( $\pm$  SE) proportion of isopod prey consumed by cunner during foraging trials among monocultures of *Chondrus crispus* ( $n = 9$ ), *Codium fragile* ssp. *fragile* ( $n = 10$ ), *Dasyisiphonia japonica* ( $n = 9$ ), *Saccharina latissima* ( $n = 9$ ), or in a control setup with no algae ( $n = 10$ ). There was no statistically significant difference in the proportion of prey consumed between treatments.

with observations by Chao (1973) suggest that the tall simple, flat-bladed structure of kelp affords protection to the resident benthic dwelling fish. In our refuge choice experiment, *U. lactuca* was chosen as a refuge more often than the filamentous alternatives. Despite the obvious differences between the green alga *U. lactuca* and the kelp *S. latissima*, the two species are similar in their general blade-like shape and low fractal dimension (Table 2). In situ observations revealed that cunner sought refuge more than foraged in habitats with greater kelp cover and sought refuge and foraged equally in turf-dominated habitats. Microhabitat selection for refuge was habitat specific with cunner hiding more in *S. latissima* in kelp and mixed habitats, but equally in *S. latissima* and *D. japonica* in turf-dominated habitats, despite *S. latissima* low percent cover in this habitat. These studies suggest that cunner prefer the tall and morphologically simple form of *S. latissima* as a refuge, but will use a shorter, more complex form when necessary.

Given our evidence that cunner do not use macroalgae indiscriminately, they will potentially be impacted by the ongoing and future changes in temperate reef ecosystems of the Gulf of Maine. Though we did not directly measure predation, our findings, along with others (e.g., Chao, 1973), provide support that adult cunner use various kelp species as shelter. Adult cunner establishes closely guarded territories, where they have access to food and shelter, and do not vacate them readily (Pottle and Green, 1979). They are fed on opportunistically by a range of animals (e.g. Ojeda and Dearborn, 1991; Nelson et al., 2003). Three of these predators, striped bass, pollock, and harbor seals, were identified in our video footage. Real threats to cunner are thus present in the surveyed habitats, increasing their need for suitable refuge spaces. Macroalgal habitats may also be important for other life-stages of cunner. For example, Tupper and Juanes (2017) found that juvenile cunner exert more energy on refuge defense when in habitats with little shelter available, and posited that access to protected refuges must be an important survival factor for cunner. Juvenile cunner are vulnerable post-settlement to predation by longhorn sculpin, grubby sculpin, and sea ravens (Tupper and Boutilier, 1997). With reduced kelp cover, we may expect to see the beginnings of density-dependent mortality in cunner populations, with available refuge as the main limiting factor, as has been shown experimentally in certain gobies (Forrester and Steele, 2004).

Greater vulnerability of both juvenile and adult cunner caused by changes in macroalgal composition may have cascading effects on other members of the Gulf of Maine ecosystem. As mid-level predators, cunner is directly linked to several important fisheries species: as predators of small green urchins, lobsters, and rock crabs; and as prey for striped bass and pollock (Bigelow and Schroeder, 1953; Ojeda and Dearborn, 1991; Bowman et al., 2000; Nelson et al., 2003). A reduction in the cunner population caused by limited shelter availability could lead to a trophic release on their small invertebrate prey.

Contrary to our expectations, algal complexity did not affect the ability of cunner to locate and consume isopod prey in our laboratory experiment. Prey capture was comparable among the treatment groups. Our findings indicate that cunner predation on isopods is not affected negatively by the shift to more complex turf algae. However, habitat-mediated interactions are complicated, and isopods are only one of many different prey items consumed by cunner. Previous research concerning predation in complex habitats shows that interactions are often dependent on species-specific traits such as the predator's hunting technique and the prey's microhabitat usage (e.g. Holmlund et al., 1990; Warfe and Barmuta, 2006; Klecka and Boukal, 2014; Grutters et al., 2015). Valley and Bremigan (2002) showed that largemouth bass attack and consumption rates were reduced in high macrophyte density treatments, while Hovel et al. (2016) found no net effect on fish predation due to the combination of decreased prey detection, but increased prey retention within more complex eelgrass habitat. The isopods used in our experiment are mobile, and while they tend to settle on macroalgae while resting or foraging, they are more than capable of swimming swiftly to escape predators (Vesakoski et al., 2008). Other

invertebrates preyed on by cunner are less active. For example, Martin (1988) found that cunner predation on caprellid amphipods (which are mainly sedentary and do not often detach from their chosen plant) was strongly reduced with increasing plant complexity. Thus, the functional trait of macroalgae complexity may influence the ability of cunner to locate some prey items but not others, dependent on the prey's behavioral mode. With the ongoing changes in the southern Gulf of Maine's macroalgae communities (Dijkstra et al., 2017), we expect that the more mobile invertebrate prey items (such as isopods and gammarid amphipods) will remain under similar predation pressure from cunner, while sedentary species which are less mobile and can blend in with the filamentous introduced macroalgae (such as caprellid amphipods) will experience less predation pressure. The ultimate community implications of this categorical alteration in predation pressure require further study.

Changes in the macroalgae assemblage in the southern Gulf of Maine resemble those occurring in other temperate reef systems around the globe, wherein taller canopy-forming species have been lost and replaced by low-growing turf algae (Connell et al., 2008; Connell and Russell, 2010; Mezaki and Kubota, 2012; Vergés et al., 2016; Wernberg et al., 2016; Dijkstra et al., 2017). Our results suggest that the loss of these foundation species may negatively affect resident fish populations through greater exposure to predators resulting from the lack of suitable biogenic refuge. In other systems, we might expect to see similar changes in refuge use (and potentially increased predator vulnerability) in fish species with characteristics similar to cunner: being primarily benthic, remaining within a small local territory, and associating closely with biogenic structure. However, community interactions are often complex and species-specific. Cheminée et al. (2017) showed that typical *Cystoseira* forests supported richer and more abundant communities of juvenile fish compared to the Dictyotales-Sphaecelariales brushland alternative. The authors noted the importance of three-dimensional structure created by *Cystoseira*, and found that canopy volume could explain some taxa-specific differences in juvenile abundance among forested sites. In contrast, Terazono et al. (2012) found that tropical *Sargassum* species with lower canopy heights supported the same species assemblage and food habits as native, taller *Sargassum*. Thus, it is important to consider the specific needs and characteristics of regional fish assemblages when assessing the impacts of structural habitat changes.

One of the goals of trait-based ecology is to identify general ecological patterns which are derivable from easily quantified characteristics of an organism, without being hindered by taxonomic identity. In the present study, we used functional traits of height, weight and complexity of macroalgae to represent the ongoing shift from large kelp species to lower turf algae in the Gulf of Maine, and its effects on the refuge and foraging of a resident benthic fish. Our results indicate that the impacts are neither wholly positive nor negative in this system. When considering cunner as a prey species for larger animals, we have found that they prefer to seek refuge in taller kelp blades but would utilize turf algae if necessary. Since we did not measure predation directly, we cannot say for certain whether or not this turf provides the same quality of shelter that kelp blades do, although we are inclined to believe that cunner are more visible among turfs which do not fully impede our view of the fish. However, when viewing cunner as predators of meso-invertebrates, the effects of macroalgae complexity on foraging success seem to be dependent on the behavioral traits of the prey species. This discrepancy highlights the intricacy of trophic interactions. When using functional traits to interpret ecological patterns, it is important to keep in mind all of the possible factors. Trait-based ecology will continue to be a powerful tool for predicting and understanding how ecosystems are affected by shifts in dominant species assemblages, both in temperate macroalgae reefs and elsewhere. Using functional traits to narrow down complex trophic interactions into their core quantifiable aspects will allow us to gain a stronger, more mechanistic understanding of how these ecosystems are changing.

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## Author contributions

JAD conceived the idea. All authors collected the data. BSO and JAD analyzed the data and performed statistical analyses. BSO led the writing with contributions from all authors.

## Data accessibility

Data will be archived at Dryad Digital Repository.

## Declarations of interest

None.

## References

- Asner, G.P., Hughes, R.F., Vitousek, P.M., Knapp, D.E., Kennedy-Bowdoin, T., Boardman, J., Martin, R.E., Eastwood, M., Green, R.O., 2008. Invasive plants transform the three-dimensional structure of rain forests. *Proc. Natl. Acad. Sci. U. S. A.* 105, 4519–4523.
- Barnes, T.G., Madison, L.A., Sole, J.D., Lacki, M.J., 1995. An assessment of habitat quality for northern bobwhite in tall fescue-dominated fields. *Source Wildl. Soc. Bull.* 23, 231–237.
- Bigelow, H.B., Schroeder, W.C., 1953. *Fishes of the Gulf of Maine*, fishery bulletin of the fish and wildlife service. Washington, DC: US Government Printing Office. <http://dx.doi.org/10.1007/s13398-014-0173-7.2>.
- Blackwell, B.F., Sinclair, J.A., 1995. Evidence of secondary consumption of fish by double-crested cormorants. *Mar. Ecol. Prog. Ser.* 123, 1–4.
- Bowman, R.E., Stillwell, C.E., Michaels, W.L., Grosslein, M.D., 2000. Food of Northwest Atlantic fishes and two common species of squid. In: U.S. Dep. Commer. Natl. Ocean. Atmos. Adm. Nation Mar. Fish. Serv. Northeast Reg. (ii-137).
- Carter, K.M., Woodley, C.M., Brown, R.S., 2011. A review of tricaine methanesulfonate for anesthesia of fish. *Rev. Fish Biol. Fish.* 21, 51–59.
- Chao, L.N., 1973. Digestive system and feeding habits of the cunner, *Tautoglabrus adspersus*, a stomachless fish. *Fish. Bull.* 71, 565–586.
- Chapman, A.R.O., Johnson, C.R., 1990. Disturbance and organization of macroalgal assemblages in the Northwest Atlantic. *Hydrobiologia* 192, 77–121.
- Cheminée, A., Pastor, J., Bianchimani, O., Thiriet, P., Sala, E., Cottalorda, J.M., Dominici, J.M., Lejeune, P., Francour, P., 2017. Juvenile fish assemblages in temperate rocky reefs are shaped by the presence of macroalgae canopy and its three-dimensional structure. *Sci. Rep.* 7, 1–11.
- Coleman, F.C., Williams, S.L., 2002. Overexploiting marine ecosystem engineers: potential consequences for biodiversity. *Trends Ecol. Evol.* 17, 40–44.
- Connell, S.D., Russell, B.D., 2010. The direct effects of increasing CO<sub>2</sub> and temperature on non-calcifying organisms: increasing the potential for phase shifts in kelp forests. *Proc. Biol. Sci.* 277, 1409–1415.
- Connell, S.D., Russell, B.D., Turner, D.J., Shepherd, S.A., Kildea, T., Miller, D., Airoldi, L., Cheshire, A., 2008. Recovering a lost baseline: missing kelp forests from a metropolitan coast. *Mar. Ecol. Prog. Ser.* 360, 63–72.
- Crooks, J.A., 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* 97, 153–166.
- Dijkstra, J.A., Harris, L.G., Mello, K., Litterer, A., Wells, C., Ware, C., 2017. Invasive seaweeds transform habitat structure and increase biodiversity of associated species. *J. Ecol.* 105, 1668–1678.
- Ellison, C., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front. Ecol. Environ.* 3, 479–486.
- Filbee-Dexter, K., Wernberg, T., 2018. Rise of turfs: a new battlefield for globally declining kelp forests. *Bioscience* XX, 1–13. <http://dx.doi.org/10.1093/biosci/bix147>.
- Forrester, G.E., Steele, M., 2004. Predators, prey refuges, and the spatial scaling of density-dependent prey mortality. *Ecology* 85, 1332–1342.
- Grabowski, J.H., Powers, S.P., 2004. Habitat complexity mitigates trophic transfer on oyster reefs. *Mar. Ecol. Prog. Ser.* 277, 291–295.
- Green, J.M., Martel, G., Martin, D.W., 1984. Comparisons of the feeding activity and diets of male and female cunners *Tautoglabrus adspersus* (Pisces: Labridae). *Mar. Biol.* 84, 7–11.
- Griffin, J.N., Mendez, V., Johnson, A.F., Jenkins, S.R., Foggo, A., 2009. Functional diversity predicts overyielding effect of species combination on primary productivity. *Oikos* 118, 37–44.

- Gross, N., Le Bagousse-Pinguet, Y., Liancourt, P., Berdugo, M., Gotelli, N.J., Maestre, F.T., 2017. Functional trait diversity maximizes ecosystem multifunctionality. *Nat. Ecol. Evol.* 1, 132.
- Grutters, B.M.C., Bart, B.J., Verberk, W.C.E.P., Bakker, E.S., 2015. Native and non-native plants provide similar refuge to invertebrate prey, but less than artificial plants. *PLoS One* 10, 1–18.
- Hall, C.S., Kress, S.W., Griffin, C.R., 2000. Composition, spatial and temporal variation of common and Arctic tern chick diets in the Gulf of Maine. *Waterbirds* 23, 430–439.
- Hammill, M.O., Stenson, G.B., 2000. Estimated prey consumption by harp seals (*Phoca groenlandica*), hooded seals (*Cystophora cristata*), grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) in Atlantic Canada. *J. Northwest Atl. Fish. Sci.* 26, 1–23.
- Heck, K.L.J., Crowder, L.B., 1991. Habitat structure and predator-prey interactions in vegetated aquatic systems. In: Bell, S.S., McCoy, E.D., Mushinsky, H.R. (Eds.), *Habitat Structure*. Springer, Netherlands, pp. 281–299.
- Holmlund, M.B., Peterson, C.H., Hay, M.E., 1990. Does algal morphology affect amphipod susceptibility to fish predation? *J. Exp. Mar. Bio. Ecol.* 139, 65–83.
- Hovel, K.A., Warneke, A.M., Virtue-Hilborn, S.P., Sanchez, A.E., 2016. Mesopredator foraging success in eelgrass (*Zostera marina* L.): relative effects of epiphytes, shoot density, and prey abundance. *J. Exp. Mar. Bio. Ecol.* 474, 142–147.
- Jänes, H., Kotta, J., Pärnoja, M., Crowe, T.P., Rindi, F., Orav-Kotta, H., 2017. Functional traits of marine macrophytes predict primary production. *Funct. Ecol.* 31, 975–986.
- Johns, P.M., Mann, K.H., 1987. An experimental investigation of juvenile lobster habitat preference and mortality among habitats of varying structural complexity. *J. Exp. Mar. Bio. Ecol.* 109, 275–285.
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69, 373–386.
- Klecka, J., Boukal, D.S., 2014. The effect of habitat structure on prey mortality depends on predator and prey microhabitat use. *Oecologia* 176, 183–191.
- Kunstler, G., Falster, D., Coomes, D.A., Hui, F., Kooyman, R.M., Laughlin, D.C., Poorter, L., Vanderwel, M., Vieilledent, G., Wright, S.J., Aiba, M., Baraloto, C., Caspersen, J., Cornelissen, J.H.C., Gourlet-Fleury, S., Hanewinkel, M., Herauld, B., Kattge, J., Kurokawa, H., Onoda, Y., Peñuelas, J., Poorter, H., Uriarte, M., Richardson, S., Ruiz-Benito, P., Sun, L.-F., Ståhl, G., Swenson, N.G., Thompson, J., Westerlund, B., Wirth, C., Zavala, M.A., Zeng, H., Zimmerman, J.K., Zimmermann, N.E., Westoby, M., 2015. Plant functional traits have globally consistent effects on competition. *Nature* 529, 204–207.
- Lawton, J.H., 1983. Plant architecture and the diversity of phytophagous insects. *Annu. Rev. Entomol.* 28, 23–29.
- Levin, P.S., Coyer, J.A., Petrik, R., Good, T.P., 2002. Community-wide effects of non-indigenous species on temperate rocky reefs. *Ecology* 83, 3182–3193.
- MacArthur, R.H., MacArthur, J.W., 1961. On bird species diversity. *Ecology* 42, 594–598.
- Martin, P.D., 1988. The Ecology of Caprellid Ampipods: Population Patterns and the Role of Algal Complexity in Mediating Predation by Wrasse. University of New Hampshire.
- McCoy, E.D., Bell, S.S., 1991. Habitat Structure: the evolution and diversification of a complex topic. In: Bell, S.S., McCoy, E.D., Mushinsky, H.R. (Eds.), *Habitat Structure: The Physical Arrangement of Objects in Space*. Chapman & Hall, London, pp. 3–27.
- McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* 21, 178–185.
- McIntyre, P.J., Thorne, J.H., Dolanc, C.R., Flint, A.L., Flint, L.E., Kelly, M., Ackerly, D.D., 2015. Twentieth-century shifts in forest structure in California: denser forests, smaller trees, and increased dominance of oaks. *Proc. Natl. Acad. Sci. U. S. A.* 112, 1458–1463.
- Mezaki, T., Kubota, S., 2012. Changes of hermatypic coral community in coastal sea area of Kochi, high-latitude, Japan. *Aquabiology* 201, 332–337.
- Nagelkerken, I., Blaber, S.J.M., Bouillon, S., Green, P., Haywood, M., Kirton, L.G., Meynecke, J.O., Pawlik, J., Penrose, H.M., Sasekumar, A., Somerfield, P.J., 2008. The habitat function of mangroves for terrestrial and marine fauna: a review. *Aquat. Bot.* 89, 155–185.
- Nelson, G.A., Chase, B.C., Stockwell, J., 2003. Food habits of striped bass (*Morone saxatilis*) in coastal waters of Massachusetts. *J. Northwest Atl. Fish. Sci.* 32, 1.
- Nelson, S.B., Coon, J.J., Duchardt, C.J., Fischer, J.D., Halsey, S.J., Kranz, A.J., Parker, C.M., Schneider, S.C., Swartz, T.M., Miller, J.R., 2017. Patterns and mechanisms of invasive plant impacts on North American birds: a systematic review. *Biol. Invasions* 19, 1547–1563.
- Ojeda, F.P., Dearborn, J.H., 1991. Feeding ecology of benthic mobile predators: experimental analyses of their influence in rocky subtidal communities of the Gulf of Maine. *J. Exp. Mar. Bio. Ecol.* 149, 13–44.
- Olla, B.L., Bejda, A.J., Martin, A.D., 1975. Activity, movements, and feeding behavior of the cunner, *Tautoglabrus adspersus*, and comparison of food habits with young tautog, *Tautoga onitis*, off Long Island, New York. *Fish. Bull.* 73.
- Orth, R.J., Heck, K.L.J., van Montfrans, J., 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator: prey relationships. *Estuar. Coasts* 7, 339–350.
- Pershing, A.J., Alexander, M.A., Hernandez, C.M., Kerr, L.A., Le Bris, A., Mills, K.E., Nye, J.A., Record, N.R., Scannell, H.A., Scott, J.D., Sherwood, G.D., Thomas, A.C., 2015. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Science* (80-) 350, 809–812.
- Posey, M.H., 1988. Community changes associated with the spread of an introduced seagrass, *Zostera japonica*. *Ecology* 69, 974–983.
- Pottle, R.A., Green, J.M., 1979. Territorial behavior of the north temperate labrid, *Tautoglabrus adspersus*. *Can. J. Zool.* 57, 2337–2347.
- Ramsay-Newton, C., Drouin, A., Hughes, A.R., Bracken, M.E.S., 2017. Species, community, and ecosystem-level responses following the invasion of the red alga *Dasyatisphonia japonica* to the western North Atlantic Ocean. *Biol. Invasions* 19, 537–547.
- Rotenberry, J.T., Wiens, J.A., 1980. Habitat structure, patchiness, and avian communities in north american steppe vegetation: a multivariate analysis. *Ecology* 61, 1228–1250.
- Sanders, D., Nickel, H., Grützner, T., Platner, C., 2008. Habitat structure mediates top-down effects of spiders and ants on herbivores. *Basic Appl. Ecol.* 9, 152–160.
- Schmidt, A.L., Coll, M., Romanuk, T.N., Lotze, H.K., 2011. Ecosystem structure and services in eelgrass *Zostera marina* and rockweed *Ascophyllum nodosum* habitats. *Mar. Ecol. Prog. Ser.* 437, 51–68.
- Schneider, C.W., 2010. Report of a new invasive alga in the Atlantic United States: “*Heterosiphonia*” *japonica* in Rhode Island. *J. Phycol.* 46, 653–657.
- Smith, D.M., Finch, D.M., 2013. Use of native and nonnative nest plants by riparian-nesting birds along two streams in New Mexico. *River Res. Appl.* 30, 1134–1145.
- Steneck, R.S., Leland, A., McNaught, D.C., Vavrinc, J., 2013. Ecosystem flips, flops, and feedbacks: the lasting effects of fisheries on Miane’s kelp forest ecosystem. *Bull. Mar. Sci.* 89, 31–55.
- Teagle, H., Hawkins, S.J., Moore, P.J., Smale, D.A., 2017. The role of kelp species as biogenic habitat formers in coastal marine ecosystems. *J. Exp. Mar. Bio. Ecol.* 492, 81–98.
- Terazono, Y., Nakamura, Y., Imoto, Z., Hiraoka, M., 2012. Fish response to expanding tropical Sargassum beds on the temperate coasts of Japan. *Mar. Ecol. Prog. Ser.* 464, 209–220.
- Thomson, J.A., Burkholder, D.A., Heithaus, M.R., Fourqurean, J.W., Fraser, M.W., Statton, J., Kendrick, G.A., 2015. Extreme temperatures, foundation species, and abrupt ecosystem change: an example from an iconic seagrass ecosystem. *Glob. Chang. Biol.* 21, 1463–1474.
- Tupper, M.H., Boutlier, R., 1997. Effects of habitat on settlement, growth, predation risk and survival of a temperate reef fish. *Mar. Ecol. Prog. Ser.* 151, 225–236.
- Tupper, M., Juanes, F., 2017. Testing foraging arena theory: the effects of conspecific density and habitat type on time and energy budgets of juvenile cunner. *J. Exp. Mar. Bio. Ecol.* 487, 86–93.
- Valley, R.D., Bremigan, M.T., 2002. Effects of macrophyte bed architecture on Largemouth Bass foraging: implications of exotic macrophyte invasions. *Trans. Am. Fish. Soc.* 131, 234–244.
- Verberk, W.C.E.P., van Noordwijk, C.G.E., Hildrew, A.G., 2013. Delivering on a promise: integrating species traits to transform descriptive community ecology into a predictive science. *Freshw. Sci.* 32, 531–547.
- Vergés, A., Doropoulos, C., Malcolm, H.A., Skye, M., Garcia-Pizá, M., Marzinelli, E.M., Campbell, A.H., Ballesteros, E., Hoey, A.S., Vila-Concejo, A., Bozec, Y.-M., Steinberg, P.D., 2016. Long-term empirical evidence of ocean warming leading to tropicalization of fish communities, increased herbivory, and loss of kelp. *Proc. Natl. Acad. Sci. U. S. A.* 113, 13791–13796.
- Vesakoski, O., Merilaita, S., Jormalainen, V., 2008. Reckless males, rational females: dynamic trade-off between food and shelter in the marine isopod *Idotea balthica*. *Behav. Process.* 79, 175–181.
- Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional!. *Oikos* 116, 882–892.
- Warfe, D.M., Barmuta, L.A., 2004. Habitat structural complexity mediates the foraging success of multiple predator species. *Oecologia* 141, 171–178.
- Warfe, D.M., Barmuta, L.A., 2006. Habitat structural complexity mediates food web dynamics in a freshwater macrophyte community. *Oecologia* 150, 141–154.
- Webb, C.T., Hoeting, J.A., Ames, G.M., Pyne, M.I., LeRoy Poff, N., 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecol. Lett.* 13, 267–283.
- Wernberg, T., Smale, D.A., Tuya, F., Thomsen, M.S., Langlois, T.J., de Bettignies, T., Bennett, S., Rousseaux, C.S., 2013. An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nat. Clim. Chang.* 3, 78–82.
- Wernberg, T., Bennett, S., Babcock, R.C., De Bettignies, T., Cure, K., Depczynski, M., Dufois, F., Fromont, J., Fulton, C.J., Hovey, R.K., Harvey, E.S., Holmes, T.H., Kendrick, G.A., Radford, B., Santana-garcon, J., Saunders, B.J., Smale, D.A., Thomsen, M.S., Tuckett, C.A., Tuya, F., Vanderklift, M., Wilson, S., 2016. Climate-driven regime shift of a temperate marine ecosystem. 353. pp. 169–172.
- Witman, J.D., Lamb, R.W., 2018. Persistent differences between coastal and offshore kelp forest communities in a warming Gulf of Maine. *PLoS One* 13, e0189388.
- Wright, J.T., Byers, J.E., DeVore, J.L., Sotka, E.E., 2014. Engineering or food? Mechanisms of facilitation by a habitat-forming invasive seaweed. *Ecology* 95, 2699–2706.