



# Fish and seagrass communities vary across a marine reserve boundary, but seasonal variation in small fish abundance overshadows top-down effects of large consumer exclosures

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## ABSTRACT

A growing number of examples indicate that large predators can alter seagrass ecosystem structure and processes via top-down trophic interactions. However, the nature and strength of those interactions varies with biogeographic context, emphasizing the need for region-specific investigations. We investigated spatial and temporal variation in predatory fish and seagrass communities across a Marine Protected Area (MPA) boundary in the Banana River Lagoon, Florida (USA), assessing trophic roles of intermediate consumers, and performing a large-consumer exclusion experiment in the MPA. Large, predatory fishes were most abundant within the MPA, while some mid-sized fishes were more abundant outside it. Small, seagrass-resident fishes, epifaunal invertebrates, and macrophytes also differed across the MPA boundary, but varied more among individual sites and seasonally. We cannot conclusively attribute these patterns to MPA status because we lack data from prior to MPA establishment and lack study replication at the level of MPA. Nevertheless, other patterns among our data are consistent with hypothesized mechanisms of top-down control. E.g., inverse seasonal patterns in the abundance of organisms at adjacent trophic levels, coupled with stable C and N isotope and gut contents data, suggest top-down control of crustacean grazers by seasonal recruitment of small fishes. Large-consumer exclosures in the MPA increased the abundance of mid-sized predatory and omnivorous fishes, but had few impacts on lower trophic levels. Results suggest that large-scale variation in large, predatory fish abundance in this system does not strongly affect seagrass-resident fish, invertebrate, and algal communities, which appear to be driven more by habitat structure and seasonal variation in small fish abundance.

## 1. Introduction

Seagrasses occur worldwide in shallow marine and estuarine waters (Hemminga and Duarte, 2000) where they enhance biodiversity and contribute to vital ecosystem functions such as sediment stabilization and primary and secondary production (Edgar and Shaw, 1995; Worm et al., 2006). Unfortunately, seagrass is declining in many regions (Orth et al., 2006; Waycott et al., 2009). These declines are typically linked to water quality degradation and other anthropogenic changes in the physical environment (Duarte, 2002; Kemp et al., 2005; Yarbrow and Carlson, 2015), but overharvest of large consumers has also been hypothesized to impact seagrass health, via direct and indirect trophic

effects (Jackson et al., 2001; Heck and Valentine, 2007). Correlative and experimental evidence of these trophic effects is accumulating, suggesting that top-down controls on seagrass abundance are highly influential but vary among different seagrass ecosystems (Duffy et al., 2013; Östman et al., 2016).

The proximal mechanism of trophic influence on seagrass health is herbivory, of which two types are important: 1) *Direct grazing* sometimes harms seagrass, but may also increase seagrass production by removing older, epiphyte-covered blades thereby increasing the availability of light and nutrients (Valentine and Duffy, 2006). 2) *Epiphyte grazing* selectively removes algal competitors and usually benefits seagrass (Jernakoff et al., 1996). Mesocosm and field experiments

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manipulating herbivores show that the magnitude of both kinds of grazing effects is often equal to or greater than the magnitude of nutrient enrichment effects (Hughes et al., 2004; Duffy et al., 2015; Östman et al., 2016), and that reduced abundance or activity of epiphyte grazers is likely a pre-condition for eutrophic epiphyte overgrowth (Neckles et al., 1993; Heck and Valentine, 2007). A growing number of experiments have also manipulated small predators and demonstrated cascading top-down effects through grazers to the level of epiphytes and seagrass (Duffy et al., 2005; Douglass et al., 2007; Moksnes et al., 2008; Reynolds et al., 2014).

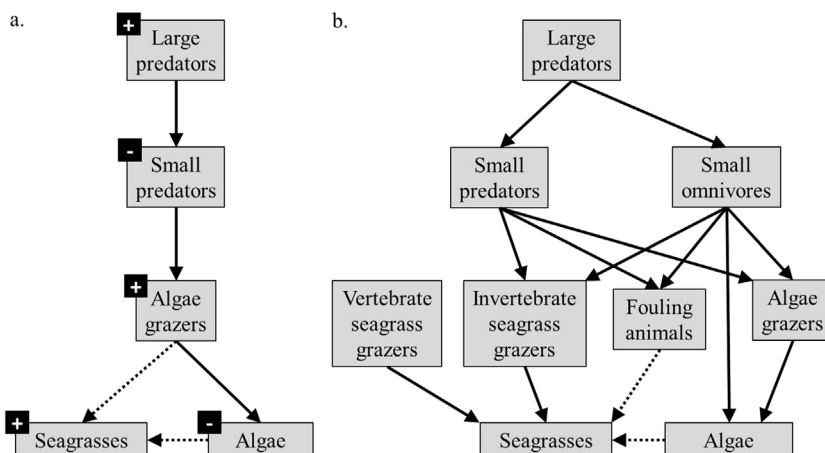
Consumer manipulations have historically focused on small, seagrass-resident predators, and have rarely included the larger predatory species directly impacted by overfishing. However, the potential for overfishing to have harmful, indirect effects on seagrasses has recently been demonstrated in tropical systems where direct grazing dominates (e.g., Burkholder et al., 2013; Heithaus et al., 2014), and in temperate systems where epiphyte grazing is predominant (Eriksson et al., 2009; Sieben et al., 2011; Baden et al., 2012, others reviewed in Östman et al., 2016). In the tropical systems, it is inferred that shark presence indirectly increases seagrass biomass by reducing sirenian and sea turtle grazing activity. In the temperate examples there is a four-level trophic cascade from piscivorous fishes, to small, seagrass-resident fishes, to invertebrate mesograzers, to ephemeral epiphytic algae, which compete with seagrasses for light (Fig. 1a). Despite these compelling examples, wide variation in seagrass foodweb structure around the world makes it challenging to apply simplistic models of top-down control across different seagrass systems, even within the temperate zone (Duffy et al., 2013, 2015, Fig. 1b). Whether reduction of large consumers has negative, positive, or negligible effects on a particular seagrass system likely depends on the structure of the seagrass foodweb, including the number of trophic levels and the functional diversity at each trophic level (Östman et al., 2016). High taxonomic and functional diversity of grazers appears to strengthen grazer control of algae (Duffy et al., 2015), but may increase grazer community resistance to predation (Duffy, 2002) and thereby reduce the likelihood of community-wide trophic cascades (sensu Polis and Strong, 1996) from predators to algae and seagrass. For example, gastropod mesograzers appear less susceptible to top-down control than crustacean mesograzers (Östman et al., 2016), and the gastropod:crustacean ratio of mesograzer communities varies among regions (Duffy et al., 2015), suggesting that trophic cascade susceptibility may vary accordingly. However, even if community-wide trophic cascades do not occur in a particular seagrass system, reduction of large consumers could still effect cascading changes at the level of key species and functional groups, as demonstrated by predator exclusion experiments in The Bahamas (Hammerschlag-Peyer et al., 2013). To effectively incorporate top-down ecology in global seagrass conservation and restoration, a more detailed, region-specific understanding of the top-down interactions is needed. Significant progress

has been made toward this end by global experimental networks (Duffy et al., 2015) and meta-analyses (Östman et al., 2016), but further advances in our system-specific and general understanding can be gained by additional manipulative experiments and field comparisons, particularly those incorporating top trophic levels.

Large-scale field experiments incorporating higher trophic levels would be ideal for assessing the connections between small, seagrass-resident species and the larger consumers prone to overharvesting (Sieben et al., 2011). However, manipulating the abundance of big, highly-mobile organisms in the field is difficult. Another obstacle is that most coastal and estuarine ecosystems where seagrass occurs have already experienced major trophic restructuring as a result of overharvesting (Jackson et al., 2001), making it difficult to define appropriate control treatments in large-consumer manipulations.

A number of the problems with assessing impacts of large consumers on seagrass community structure and trophic processes could be avoided by working within well-established marine protected areas (MPAs). Working within an MPA allows upper trophic level manipulation by exclusion; simulating overfishing-related trophic changes within an enclosure while a control environment with large consumers exists outside the enclosure. Marine protected areas are increasingly being used as tools for fisheries management and biodiversity conservation (Micheli et al., 2004), and they have shown promise for restoring structure and function to hard-bottom benthic habitats via indirect trophic pathways (Pinnegar et al., 2000; Aronson and Precht, 2006; Guidetti and Sala, 2007). Although the restoration of soft-bottom seagrass habitats is not a common justification for MPA establishment, some MPAs do include extensive seagrass beds. These are the ideal locations for studying the influence of anthropogenic food web alteration on seagrass health and determining whether protections on large consumer species could help conserve seagrass by promoting beneficial types of grazing.

The John F. Kennedy Space Center (KSC, Florida, USA) surrounds an approximately 4000 ha area of warm temperate coastal lagoon that, for national security and public safety reasons, and later as part of the Merritt Island National Wildlife Refuge (MINWR), has been a fully and rigorously enforced no-take marine protected area since 1962 (Johnson et al., 1999). Unfortunately, there were no fish or seagrass surveys at the MPA site prior to its protection in 1962, and there are no other MPAs in the region. Thus, it is not possible in this region to assess the MPA effect, per se; only to demonstrate that the area is now characterized by a relatively high abundance of large, demersal fishes, with populations skewed demographically toward older, larger individuals (Roberts et al., 2001). Johnson et al. (1999) found the predatory sportfishes *Sciaenops ocellatus* L., *Pogonias cromis* L., and *Centropomus undecimalis* Bloch to be 6.3, 12.8, and 5.3 times more abundant, respectively, within the MPA than in fished areas of the same lagoon system. These fishes feed on smaller “meso-predators,” including



**Fig. 1.** Conceptual models of top-down trophic influences on seagrass, adapted from Duffy et al. (2013). Solid lines indicate direct trophic effects, and dotted lines indicate non-trophic effects such as competition or facilitation. a) Simple linear cascade model with four, discrete trophic levels. Plus and minus signs indicate the sign of the direct or indirect effect of large predators on the focal trophic level. b) Composite model of more complex trophic relationships documented in some, especially tropical, seagrass systems.

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