STRUCTURAL COMPLEXITY, SEASCAPE PATCHINESS, AND BODY SIZE INTERACTIVELY MEDIATE SEAGRASS HABITAT VALUE FOR A FISH MESOPREDATOR

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by

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Structural Complexity, Seascape Patchiness, and Body Size Interactively Mediate

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ABSTRACT OF THE THESIS

Structural Complexity, Seascape Patchiness, and Body Size
Interactively Mediate Seagrass Habitat Value for a Fish
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by
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Master of Science in Biology with a Concentration in Ecology
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Seagrasses form important coastal habitats that promote the foraging and survival of mesopredators. Variation in seagrass habitat structure at local and seascape scales mediates foraging success and survival, but the interactive effects of structure at these scales rarely is quantified when evaluating nursery habitat function. For my thesis, I tested how the interactions of multiscale habitat structural variation on juvenile fish body size mediates the value of seagrass habitat through survival and foraging success.

In Chapter 1, I tested the hypothesis that in eelgrass (Zostera marina) optimal structural complexity (SC) for juvenile giant kelpfish (Heterostichus rostratus) changes through ontogeny. I found that habitat selection differed with kelpfish size: small and large fish selected high and low SC respectively. Smaller kelpfish experienced lower predation risk and higher foraging in high SC, suggesting high SC is selected by these fish because it minimizes risk and maximizes growth potential. Larger kelpfish experienced lower predation risk and higher foraging in high and low SC respectively, suggesting they select low SC to maximize foraging efficiency. My study highlights that trade-offs between predation risk and foraging can occur within a single habitat type, that studies should consider how habitat value changes through ontogeny, and that seagrass nursery habitat value may be maximal when within-patch variability in SC is high.

In Chapter 2, I used a spatially explicit individual-based model to examine how seagrass fragmentation influences foraging and survival of a mesopredator, and how these relationships are influenced by SC, body size, and mesopredator and prey densities. I found that mesopredator survival and foraging dropped beyond threshold levels of habitat area (60 and 30% respectively) and depended on level of SC in the seascape. The relationship between habitat area and foraging did not depend on SC or body size, but did depend on organismal densities: when mesopredators and prey densities increased with decreasing habitat area, foraging was highest in highly fragmented seascapes. My results suggest that small- and large-scale habitat structure jointly dictate the value of a nursery habitat, and the effects of survival and foraging should consider interactions with habitat structure at multiple scales.

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CHAPTER 1

EELGRASS HABITAT VALUE: STRUCTURAL COMPLEXITY AND FISH BODY SIZE INTERACTIVELY AFFECT HABITAT OPTIMALITY

INTRODUCTION

Predator-prey interactions are strongly influenced by habitat structure (Gause et al 1936; Huffaker 1958; Holt 1987). The amount, density, and diversity of structural elements in a habitat dictate predator-prey encounter rates, capture success for predators, and habitat refuge value for prey (Crowder and Cooper 1982; Heck and Crowder 1991; Hixon and Beets 1993; Hughes and Grabowski 2006). Mesopredators are mid-trophic level consumers that must simultaneously search for prey and avoid being captured by higher-order predators. Therefore, variability in habitat structure may alter the value of habitat for mesopredators, and their selection of habitat, in complex ways. For instance, in the presence of a predatory threat mesopredators may select patches of high habitat structure to maximize refuge value and survival (Schmitt and Holbrook 1985), but may experience reduce foraging efficiency due to decreased mobility and detection of prey where structural elements are dense (Gotceitas and Colgan 1989). In contrast, lower density patches offering better foraging opportunities, but less refuge, may be selected when perceived mortality risks are lower (Gotceitas 1990). Trade-offs in habitat use such as these may be common in marine habitats, where prey abundance often is positively correlated with structural complexity.

Optimality models predict that mesopredators use structured habitats in ways that minimize the ratio of predation risk (μ) to food intake and growth (g), thereby maximizing fitness (Werner and Gilliam 1984; Werner and Hall 1988; Gotceitas 1990; Dahlgren and

Eggleston 2000; Kimirei et al. 2013). Because relationships between habitat structure, predation risk, and foraging efficiency are greatly affected by mobility and body size (Bartholomew et al. 2000), optimality models also predict that fitness is maximized by selection of different habitats as organisms grow. For example, juvenile American lobsters (*Homarus americanus*) are sedentary within small cobble shelters with high refuge value after recruitment, but are found foraging within a wider variety of habitats as older juveniles (Wahle and Steneck 1991, 1992). Similarly, newly recruited juvenile Nassau grouper (*Epinephelus striatus*) occupy algal habitats where they experience minimal mortality risk but fewer foraging opportunities, but after reaching a size refuge shift to post-algal habitats that promote higher foraging efficiency (Dalhgren and Eggleston 2000). Although optimality models have been used to examine apparent ontogenetic habitat shifts among habitat types, little is known about whether similar shifts occur within a single habitat due to potential trade-offs between predation risk and growth arising from local-scale heterogeneity in habitat structure.

Seagrasses, found along many of the world's shallow marine coastlines, provide a variety of critical ecosystem services including stabilizing sediments, promoting biodiversity, and serving as nursery habitats for the juveniles of many commercially and recreationally-important fauna (Williams and Heck 2001; Orth et al. 2006; McGlathery et al. 2007). Seagrass habitat structure varies temporally and spatially at a variety of scales, and strongly influences predator-prey interactions (Irlandi 1994; Jones et al. 2013), epifaunal biomass (Tanner 2005; Moore and Hovel 2010), and organismal behavior (Spitzer et al. 2000; Tait and Hovel 2012). Within patches (i.e., at the scale of meters), structural complexity (e.g., shoot density, surface area, length, or biomass per unit area; hereafter "SC") may be highly variable. At landscape scales, patchiness and fragmentation of seagrass beds results from animal foraging, bioturbation, scouring by waves and currents, and anthropogenic activity such as trampling, propeller scarring, and vessel groundings (Sargent et al. 1995). At a global scale, eutrophication, fishing, sedimentation, and disease have resulted in a loss of approximately 30% of seagrass habitat since 1990 (Short and Wyllie-Echeverria 1996; Waycott et al. 2009). In light of the rapid rate of seagrass loss and fragmentation, it is critical to understand how changes in seagrass structure impact associated fauna.

In this study, I examine whether eelgrass (*Zostera marina*) SC and fish body size interactively dictate habitat selection, mortality risk, and foraging efficiency for an abundant mesopredator in southern California, the juvenile giant kelpfish (*Heterostichus rostratus*; hereafter "kelpfish"). Eelgrass, one of about 50 species of seagrasses worldwide, is one of the most widespread marine macrophytes and provides refuge and foraging habitat for many vertebrate and invertebrate mesopredators. Though many studies have addressed the effects of eelgrass SC on predator-prey dynamics (e.g., Heck and Crowder 1991; Irlandi 1994; Hovel and Lipcius 2001; Kelecka and Boukal 2014), experiments frequently focus on a particular stage of ontogeny, and rarely simultaneously test how predation risk, foraging ability, and habitat selection vary over a range of organismal body sizes. High eelgrass SC may provide refuge to newly settled small fish that can forage efficiently through small interstitial spaces, but may impede foraging for larger fish by interfering with movement and prey detection (Bartholomew 2002). In contrast, low seagrass SC may provide less cover and increase predation risk for newly settled fish, whereas larger juveniles may obtain a size refuge from gape-limited predators and experience more efficient foraging where seagrass is sparse. Thus, I predicted that optimal levels of eelgrass SC change with increasing fish body size, and that trade-offs between predation risk and foraging efficiency may occur for medium-sized fish (Figure 1).

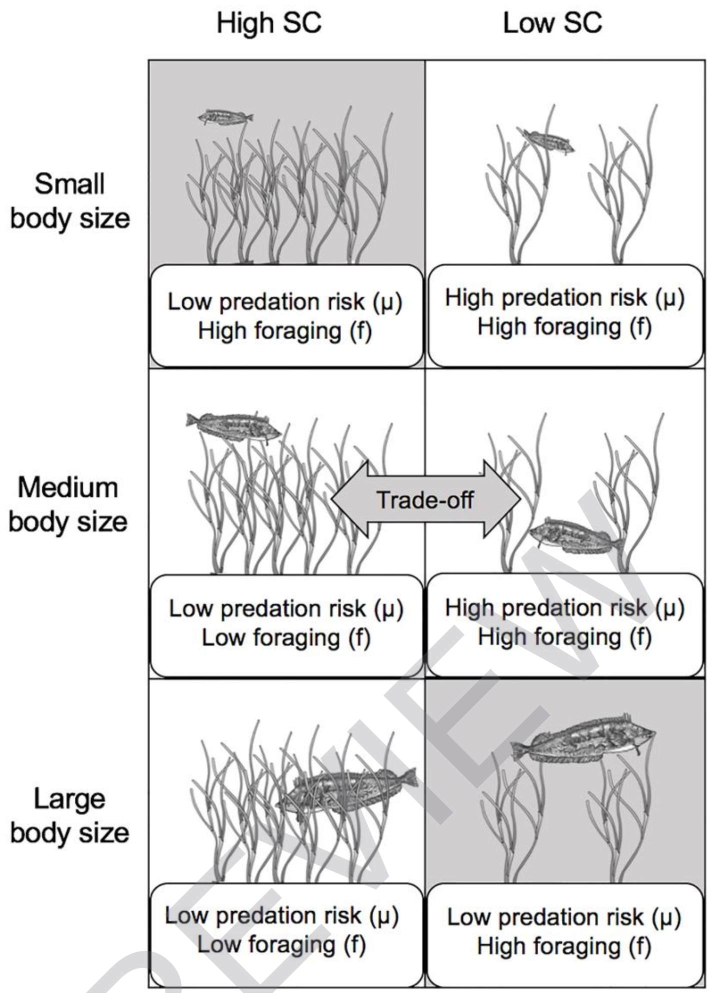

Figure 1. Conceptual model of how organism body size interacts with eelgrass structural complexity (SC) to mediate predation risk and foraging efficiency for juvenile fish. The hypothetical optimal level of SC is shown in gray for newly recruited fish and older, larger juveniles. For medium-sized fish, the model predicts that neither low nor high SC will be optimal for but that each level of SC offers different resources.