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Distribution and relative predation risk of nekton reveal complex edge effects within temperate seagrass habitat

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ABSTRACT

Edge effects may be important drivers of community dynamics across marine habitat mosaics. Past research has consistently suggested that within temperate and sub-tropical seagrass habitats, organisms inhabiting meadow edges experience lower survivorship, presumably correlated with increased predation. However, these survivorship trends have not consistently translated to differences in faunal densities between edge and interior regions of seagrass meadows. We evaluated the evidence of edge effects on predation upon two dominant mesopredators within temperate eelgrass (*Zostera marina*) communities of the U.S. East Coast: blue crabs (*Callinectes sapidus*) and pinfish (*Lagodon rhomboides*). We considered three lines of data to arbitrate the null hypothesis that edge has no impact on distribution or predation on blue crabs or pinfish: (1) relative density as measured by catch-per-unit-effort (CPUE) of blue crabs and pinfish within edge (< 1 m from unstructured sandflat boundaries) versus interior (> 3 m from unstructured sandflat boundaries) regions of eelgrass meadows; (2) distribution of acoustically tagged red drum (*Sciaenops ocellatus*), a recognized predator of both blue crabs and pinfish, within eelgrass meadows (at 1-m bin resolution); and (3) relative mortality of tethered blue crabs and pinfish within edge versus interior regions of eelgrass meadows. Additionally, we manipulated seagrass shoot density to evaluate potential interactions between local habitat complexity and edge effects. We found no statistically detectable difference in catch rates of blue crabs or pinfish in edge versus interior habitats, and red drum detection frequencies were statistically indistinguishable moving from the seagrass-sandflat boundary toward the meadow interior. Despite these findings, we did record statistically and ecologically significant edge effects on predation rates of tethered blue crabs and pinfish. Counter to previous work, we found that blue crabs survived > 2.5× longer, and pinfish survived > 2× longer, along the meadow edge relative to interior. Furthermore, the strength of these predation-related edge effects was most notable for blue crabs within plots with higher shoot density, while the opposite pattern was true for pinfish. These findings are, in part, consistent with the dichotomy apparent in the seagrass literature with respect to edge effects on faunal density and survivorship. Additionally, our work provides new detail on how habitat edges may affect the population ecology of larger bodied, more mobile mesopredator species that have not received as much attention in previous studies (i.e., higher survivorship possible along edges).

1. Introduction

Estuarine landscapes are comprised of mosaics of interconnected habitats such as mudflats, salt marshes, shellfish reefs, mangrove forests, and seagrass meadows. Along the boundaries between these habitats, edge effects may manifest as differences in the density, biomass, settlement, growth, or survivorship of flora and fauna between the interior versus outer margin (i.e., edge) of a habitat patch (Jelbart et al., 2006; Johnson and Heck, 2006; Murcia, 1995; Ries et al., 2004). In marine habitats, these differences may arise following from gradients in

flow (e.g., food or larval supply; Carroll et al., 2012) or predator accessibility (Smith et al., 2011) along an axis moving from the habitat boundary into the interior. Still, evidence regarding the direction (i.e., negative, positive) of impact of edges on resident organisms is equivocal, with many examples of fitness being depressed (Shulman, 1985; Amortegui-Torres et al., 2013), enhanced (Baltz et al., 1993; Peterson and Turner, 1994), or insensitive (Hindell and Jenkins, 2005 [Biomass]) with regard to proximity to habitat boundaries.

When focusing within individual estuarine habitats, however, more consistent edge effects may emerge. Seagrass, for example, is one of the

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Table 1

Summary table of studies examining potential edge effects on the density and survival of seagrass-associated fauna.

Study	Seagrass	Location	Taxa	Edge distance	Response variable	Conclusion
Hovel and Lipcius, 2002	<i>Z. marina</i>	Virginia (USA)	Crustaceans	< 1 m	Density	Edge < Interior
Bell et al., 2001	<i>H. wrightii</i> , <i>T. testudinum</i>	Florida (USA)	Polychaetes	< 1 m	Density	Edge < Interior
Johnson and Heck, 2006	<i>H. wrightii</i> , <i>T. testudinum</i>	Florida, Alabama (USA)	Crustaceans	< 1 m	Density	Edge < Interior
Hovel et al., 2002	<i>H. wrightii</i> , <i>T. testudinum</i>	North Carolina (USA)	Fishes	Undefined	Density	Edge < Interior
Carroll et al., 2012	ASU	New York (USA)	Bivales	< 1 m	Density	Edge > Interior
Macreadie et al., 2010	ASU	South Australia (AUS)	Fishes	< 0.5 m	Density	Edge > Interior
Macreadie et al., 2010	ASU	South Australia (AUS)	Crustaceans	< 0.5 m	Density	Edge > Interior
Moore and Hovel, 2010	<i>Z. marina</i>	California (USA)	Epifauna	< 1 m	Density	Edge > Interior
Moore and Hovel, 2010	ASU Caging	California (USA)	Epifauna	< 0.5 m	Density	Edge > Interior
Smith et al., 2008	<i>H. nigricaulis</i>	South Australia (AUS)	Fishes	< 1 m	Density	Edge > Interior
Warry et al., 2009	<i>H. nigricaulis</i>	Port Phillip Bay (AUS)	Many taxa	0 m	Density	Edge > Interior
Bologna and Heck, 1999	<i>T. testudinum</i>	Florida (USA)	Bivales	< 1 m	Density	Edge > Interior
Eggleston et al. 1998	<i>Z. marina</i> , <i>H. wrightii</i>	North Carolina (USA)	Crustaceans	Undefined	Density	Edge > Interior
Eggleston et al. 1998	ASU	North Carolina (USA)	Crustaceans	Undefined	Density	Edge > Interior
Moore and Hovel, 2010	<i>Z. marina</i>	California (USA)	Fishes	< 2 m	Density	Edge = Interior
Bologna and Heck, 2002	<i>T. testudinum</i>	Florida (USA)	Multiple invert Taxa	< 0.5 m	Density	Edge > < = Interior
Jelbart et al., 2006	<i>Z. capricorni</i>	Sydney (AUS)	Fishes	< 4 m	Density	Edge ≤ Interior
Boström et al., 2006	Multiple species	Global	Multiple invert taxa	Undefined	Density	Edge ≥ Interior
Tanner, 2005	<i>Zostera</i>	South Australia (AUS)	Multiple invert taxa	< 1 m	Density	Edge ≥ Interior
Smith et al., 2011	<i>H. nigricaulis</i>	South Australia (AUS)	Fish	< 1 m	Density	Edge > < Interior
Carroll et al., 2012	ASU	New York (USA)	Bivales	< 1 m	Survivorship	Edge < Interior
Peterson et al., 2001a, 2001b	<i>Z. marina</i>	Maine, Florida (USA)	Crustaceans	< 2 m	Survivorship	Edge < Interior
Gorman et al., 2009	<i>Z. marina</i>	Newfoundland (CAN)	Fish	0 m	Survivorship	Edge < Interior
Hovel and Lipcius, 2002	<i>Z. marina</i>	Virginia (USA)	Crustaceans	< 1 m	Survivorship	Edge < Interior
Smith et al., 2011	<i>H. nigricaulis</i>	South Australia (AUS)	Fish	< 1 m	Survivorship	Edge < Interior
Bologna and Heck, 1999	<i>T. testudinum</i>	Florida (USA)	Bivales	< 1 m	Survivorship	Edge < Interior

Artificial sea grass (ASU).

major structurally complex, biogenic habitats in estuarine environments, and has received considerable attention in studies assessing edge effects (Boström et al., 2006). Seagrass serves as a useful model system in this context due to the diverse patch orientations observed among meadows (Boström et al., 2006; Yeager et al., 2016), clear boundaries between seagrass and unstructured sandflat habitats, as well as the presence of abundant and species-rich faunal communities (Thayer et al., 1984). In particular, the dynamics of predator-prey interactions along habitat edges, with subsequent effects on faunal density, have been scrutinized across a number of seagrass species and predator-prey combinations (Table 1). Six previous studies explicitly compared survivorship of small prey species (bivalves, crustaceans, and small fishes) in edge versus interior regions of seagrass meadows (Bologna and Heck, 1999; Carroll et al., 2012; Gorman et al., 2009; Hovel and Lipcius, 2002; Peterson et al., 2001a, 2001b; Smith et al., 2011). In every case, survivorship of these taxa was depressed along seagrass edges, presumably due to elevated predation threats (Table 1). Notably, these differences in survivorship between seagrass edge versus interior did not appear to translate reliably in to elevated bivalve, crustacean, or fish densities in interior regions of seagrass habitat relative to seagrass edges (e.g., Bell et al., 2001 versus Warry et al., 2009). Approximately two-thirds of the 20 published comparisons (allowing for taxon specific comparisons within publication) documented higher densities along seagrass edges relative to seagrass interiors (Table 1).

Several factors may contribute to this disconnect. Elevated settlement (Carroll et al., 2012) or growth rates (Bologna and Heck, 2002) within edge regions of seagrass habitat may offset relationships between survivorship and density. Indeed, the tradeoffs between resource availability and risk along edge-to-interior transects is well documented in the literature (Table 1 and references therein). However, the fitness consequences of survival generally outweigh those related to resource acquisition (sensu Heck Jr et al., 2003), and thus this dynamic is unlikely to completely explain the differences between density and survivorship patterns within seagrass meadows. Additionally, movement of seagrass-associated species between edge and interior regions within habitat patches may swamp gradients in predation pressure, attenuating the effects of spatially structured survivorship on resultant prey

density patterns. Furthermore, most previous studies within seagrass have examined survivorship of small epifauna (bivalves, mesograzing crustaceans) preyed upon by crabs and fishes that range in size between 5 and 15 cm (carapace width or total length). Notably, these mesopredatory crabs and fishes are also subject to predation by even larger fishes, birds, reptiles, and mammals that may forage differentially between edge and interior regions of habitat patches. For instance, tiger shark tracking has shown that these large mobile predators prefer seagrass edge microhabitats (Heithaus et al., 2006). Indeed, large (> 50 cm) mobile predators are often conceptualized as putative edge specialists within estuarine habitat mosaics (sensu Wirsing et al., 2007), although quantitative data on the distribution of these animals are markedly rare at landscape scales. Thus, understanding how these higher-order predators affect the survivorship and distribution of mesopredators (5–15-cm crabs and fishes) could explain why previous research has documented an obvious disconnect between the survivorship and abundance of even smaller (1–5-cm bivalves, crustaceans, and fishes) seagrass-associated fauna along edge-to-interior gradients (sensu Table 1).

Within temperate U.S. East Coast and Gulf of Mexico estuaries, red drum (*Sciaenops ocellatus*) are often anecdotally depicted - as are other large mobile fishes - as edge predators along seagrass, oyster reef, and saltmarsh habitats (Dance and Rooker, 2015). Red drum are also major predators on blue crabs (*Callinectes sapidus*) and pinfish (*Lagodon rhomboides*) (Scharf and Schlicht, 2000), which themselves function as dominant mesopredators within seagrass communities (Nifong and Silliman, 2013). Notably, blue crabs (Hovel and Lipcius, 2002) and pinfish (Hovel et al., 2002) densities have been reported as depressed along seagrass meadow edges, relative to interior regions, potentially corroborating the hypotheses that higher-order predators such as red drum exert elevated mortality of mesopredators along seagrass edges. Therefore, we examined the potential for differences in predator-prey interactions among these species between edge and interior regions of seagrass meadows to expand the functional groups (e.g., larger body size, greater mobility) represented in tests of edge effects, and potentially contribute toward the reconciliation of an existing paradox evident in previous edge studies regarding seagrass-associated faunal

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