# Joint effects of patch edges and habitat degradation on faunal predation risk in a widespread marine foundation species

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**1. Abstract**

Human activities degrade and fragment coastal marine habitats, reducing their structural complexity and making habitat edges a prevalent seascape feature. Though habitat edges frequently are implicated in reduced faunal survival and biodiversity, results of experiments on edge effects have been inconsistent, calling for a mechanistic approach to the study of edges that explicitly includes indirect and interactive effects of habitat alteration at multiple scales across biogeographic gradients. We used an experimental network spanning 17 eelgrass (*Zostera marina*) sites across the Atlantic and Pacific oceans and the Mediterranean Sea to determine (i) if eelgrass edges consistently increase faunal predation risk, (ii) whether edge effects on predation risk are altered by habitat degradation (shoot thinning), and (iii) whether variation in the strength of edge effects among sites can be explained by biogeographical variability in covarying eelgrass habitat features. Contrary to expectations, at most sites, predation risk for tethered crustaceans (crabs or shrimps) was lower along patch edges than in patch interiors, regardless of the extent of habitat degradation. However, the extent to which edges reduced predation risk, compared to the patch interior, was correlated with the extent to which edges supported higher eelgrass structural complexity and prey biomass compared to patch interiors. This suggests an indirect component to edge effects in which the impact of edge proximity on predation risk is mediated by the effect of edges on other key biotic factors. Our results suggest that studies on edge effects should consider structural characteristics of patch edges, which may vary geographically, and multiple ways that humans degrade habitats.

## 2. Introduction

Foundation species form critical refuge and foraging habitats for fauna throughout the world's ecosystems, and in doing so contribute substantially to biodiversity and the maintenance of key species interactions (Ellison et al. 2012). However, ecosystem functions provided by foundation species, particularly the provision of refuge from predators, can be altered by changes in habitat structure that occur across multiple spatial scales. Within individual habitat patches, thinning or flattening reduces the structural complexity of biogenic structures (e.g., trees, grasses, coral heads, or salt marsh stems), which may strongly influence refuge value (Alvarez-Filip et al. 2009). At landscape scales, habitat loss and fragmentation reduce connectivity and create more edges between structured and unstructured habitat. Patch edges often directly elevate faunal predation risk via high rates of predator visitation to edges (Andrén 1994), but syntheses have suggested that "edge effects" are highly variable among species, sites and habitat types (Murcia 1995, Lahti 2001, Ries et al. 2004, Gross et al. 2018). Edges also may indirectly affect predation risk because predator-prey encounter rates depend strongly on habitat structural complexity, rates of disturbance, and prey density or biomass, all of which frequently vary with edge proximity (Gates and Gysel 1978, Mills 1995, Ruffell and Didham 2016). Few studies have tested how factors that vary with edge proximity alter edge effects on ecological processes, or account for their variability. Simultaneously, experiments on the effects of structural complexity loss on fauna are common, but it is less clear by what mechanisms changing complexity influences fauna, specifically how loss of structural complexity indirectly alters relationships between ecological processes and the biotic and abiotic features of habitats, including patch edges (Harper et al. 2005). These gaps have hampered development of a comprehensive theory for the effects of habitat structure on predator-prey interactions (Kovalenko et al. 2012).

47    In marine ecosystems, refuge for juvenile fishes and invertebrates increases with the

48    amount of structural complexity that habitats such as coral reefs, seagrasses, kelp forests,

49    marshes, and bivalve reefs add to the seafloor (Heck and Crowder 1991, Kovalenko et al. 2012,

50    Lefcheck et al. 2019). Physical and biological processes frequently fragment these habitats into

51    discrete patches, making habitat edges prominent features of coastal biogenic seascapes. The

52    close proximity of these habitats to human populations promote loss of structural complexity and

53    increasing patchiness due to eutrophication, physical disturbance, sedimentation, and direct and

54    indirect effects of fishing (Orth et al. 2006). These trends are likely to be exacerbated by global

55    climate change due to the limited tolerances of many foundation species to rising ocean

56    temperature and acidification (Doney et al. 2012). Thus, maintenance of key ecosystem functions

57    in coastal marine habitats will be increasingly challenged by the combined effects of local- and

58    global-scale impacts that degrade habitat structure.

59    We used a comparative-experimental approach spanning over 30 degrees of latitude and

60    several oceanic provinces to determine the effects of habitat degradation (structural complexity

61    loss) and patch edge proximity on faunal predation risk in a widespread but heavily impacted

62    marine habitat, eelgrass (*Zostera marina*). The comparative-experimental approach, in which the

63    same experimental methodology is applied within the same habitat type simultaneously across

64    distinct sites, allowed us to control for many sources of variability that may cause much of the

65    inconsistency in edge effects (and other habitat features) among studies. Patchiness and distinct

66    edges delineating structured habitat from unvegetated sediment are common features of

67    seascapes formed by eelgrass and other seagrass species (Figure S1). Eelgrass edges are formed

68    naturally by hydrodynamic scouring, bioturbation, grazing, and variability in sunlight and

69    sediment chemistry (Fonseca and Bell 1998) but are increasingly the product of anthropogenic

70   processes occurring along urbanized coastlines (Orth et al. 2006). Moreover, biotic factors that

71   strongly influence predation risk, including structural complexity and faunal density, often vary

72   with proximity to eelgrass patch edges (Bologna and Heck 1999, Moore and Hovel 2010),

73   making eelgrass an ideal experimental model system in which to address questions about direct

74   and indirect effects of patch edges on ecological processes.

75        We took advantage of biogeographic variability in eelgrass structural complexity and

76   faunal community structure among 17 eelgrass communities spread across the coastlines of

77   North America, Europe, and Asia (Figure 1; Appendix S1: Table S1) to determine (i) if eelgrass

78   edges consistently increase faunal predation risk compared to patch interiors, (ii) whether edge

79   effects on predation risk are altered by habitat degradation (shoot thinning), and (iii) whether

80   variation in the strength of edge effects among sites can be explained by biogeographical

81   variability in covarying eelgrass habitat features.

82   **3. Methods**

83        Our work involved field-based predation assays and surveys in eelgrass habitat spanning

84   much of the biogeographic range of *Z. marina*, which is found along temperate to polar

85   coastlines throughout the Northern Hemisphere. We used tethering to determine relative

86   predation risk for locally collected organisms along patch edges and in patch interiors under

87   three levels of experimental eelgrass degradation (0, 50, and 80% shoot loss) in a crossed design.

88   Tethering measures the relative mortality rate of prey among different treatments and represents

89   risk for prey that are readily available to predators (Aronson & Heck 1995). Tethered prey at

90   each site consisted of a locally collected mesopredator species (juvenile shrimp, crab, or fish)

91   commonly found in the guts of higher consumers (Appendix S1: Table S1). We chose to allow

92   prey type to vary among sites (rather than standardizing prey among sites) in order to provide a

93    relevant measure of predation risk and edge effect strength at each site. We used our

94    observations and (where available) data on predator gut contents and prey choice to ensure that

95    taxa selected for tethering were similarly vulnerable to higher-order consumers.

96        Our experiments were conducted within an approximately eight week window (15 June

97    to 15 August) in the summer of 2015. To conduct experiments, at each site we first selected a

98    large eelgrass bed (typically > 5,000 m$^2$) in shallow water (0.5 – 1.5 m water depth at low tide)

99    with a distinct edge formed by an abrupt transition from eelgrass to unvegetated sand or mud.

100   Eelgrass edges used for the experiment at each site were always submerged (i.e. we avoided

101   edges which were exposed at low tides) and at least 5 m away from any other structured habitat.

102   Edge habitat was defined as being within eelgrass but within 1 m of the transition from eelgrass

103   to unvegetated sediment, and interior habitat was $\geq$ 5 m from this transition. We chose these

104   distances because, in seagrass, habitat edge effects on mortality and abundance of small epifauna

105   typically occur within 1 m of patch edges (Tanner 2005, Macreadie et al. 2010). Patch vegetation

106   consisted exclusively of eelgrass, except for epibionts or sparse drift algae. At each site we

107   created 21 experimental 1-m x 1-m plots along the edge and 21 identical plots within the interior

108   of the eelgrass bed. To create habitat degradation treatments, we randomly selected seven of the

109   21 plots at the edge and in the interior, and after obtaining shoot counts within these plots,

110   haphazardly pulled shoots by hand to thin each plot to 50% of its ambient shoot density, creating

111   50% habitat degradation plots. We thinned another seven randomly selected plots to 20%

112   ambient shoot density (80% habitat degradation plots) along both the edge and interior of the

113   bed, while the remaining seven plots along the edge and within the interior remained at ambient

114   shoot density.

115    Each tether consisted of a single 10 cm-long piece of monofilament (Fireline™; dia. 0.13

116    mm) tied near the top of 40 cm clear acrylic rod. We used cyanoacrylate glue to affix one

117    individual prey organism to each tether, and held tethered organisms in running seawater

118    overnight before deploying each to the center of a randomly chosen plot the next day (one

119    tethered organism per plot per trial). Organisms were deployed adjacent to at least one eelgrass

120    shoot and were free to cling to the base of shoots or rest upon the sediment surface. We kept

121    tethers short to prevent tangling around seagrass shoots, because tangling can lead to treatment-

122    specific bias (e.g., if tangling is more likely to happen in dense than in sparse seagrass).

123    However, it is possible that some mortality in our study was due to predators that normally

124    would not be able to consume the species we selected, due to limited prey mobility from short

125    tethers. We suspect this was minimal, as the species we chose to tether at each site generally rely

126    on crypsis to avoid predators. Trials lasted 24 h, at which time we retrieved acrylic rods and

127    scored each individual as alive, eaten (fragments of the carapace remaining on tether), missing,

128    or molted (entire carapace remaining on tether). We considered organisms that went missing to

129    have been consumed by predators because no organisms tethered in predator-free controls at

130    three sites (n = 20 each at Bodega Bay, Finland, and San Diego) fell off tethers after 48 h. Few

131    animals molted on tethers, and any that did were removed from the analysis. Four trials of the

132    experiment were conducted over a 7 – 10 day period at each site (N = 7 individuals per treatment

133    per trial * 6 treatments * 4 trials = 168 organisms tethered per site).

134    Immediately after trials concluded we sampled all plots within the eelgrass bed at each

135    site to quantify how factors that commonly affect faunal predation risk vary with proximity to

136    the patch edge. This included two measures of habitat structural complexity (eelgrass shoot

137    density, and the biomass of epibionts, primarily algae and sessile invertebrates that add structure

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138 by colonizing shoots), as well as the biomass of canopy-dwelling epifauna. To quantify structural

139 complexity, we (i) obtained eelgrass shoot density by counting shoots within 1 m$^2$ plots (for sites

140 with low shoot density) or within smaller 314 cm$^2$ quadrats (for sites with shoot densities above

141 100 shoots m$^{-2}$); and (ii) quantified epibiont biomass by scraping all epiphytic algae and sessile

142 epifauna from three haphazardly selected shoots from each plot. Scraped epibionts and eelgrass

143 shoots were dried at 60 °C in a drying oven and weighed to calculate epibiont biomass per unit

144 eelgrass biomass (hereafter "epibiont biomass"). To quantify the biomass of canopy-dwelling

145 epifauna we placed a 25 cm diameter, 0.5 mm mesh bag over eelgrass in a haphazardly selected

146 area of each plot and cut eelgrass at the sediment surface to collect above-ground material. This

147 technique efficiently captures relatively small seagrass epifauna (e.g., amphipods, isopods,

148 gastropods, small shrimp and crabs), but undersamples larger, mobile epifauna (e.g. larger

149 shrimp and crabs, and fishes). In the laboratory we rinsed mesh bags and shoots to remove

150 epifauna, separated crustaceans from other taxa (primarily gastropods), and dried crustaceans

151 and shoots to calculate crustacean biomass per unit eelgrass biomass (hereafter "crustacean

152 biomass") which we used in statistical models to represent the availability of alternative prey

153 surrounding tethered organisms. We chose to use crustacean biomass rather than total epifaunal

154 biomass in analyses because our tethered prey were crustaceans (except at one site), and because

155 a previous study found that in eelgrass, predation rates were far lower for gastropods than for

156 crustaceans (Reynolds et al. 2018). Additionally, exploratory analyses including gastropod

157 biomass revealed no evidence for effects on predation risk or edge effect strength.

158 <u>Data analysis</u>

159 *Predation risk within sites*. We first assessed biogeographic variability in the interactive

160 effects of habitat degradation treatment, edge proximity treatment, structural complexity (shoot

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161    density and epibiont biomass), and crustacean biomass on predation risk (i.e., the odds of being

162    consumed). At each site we used a model comparison approach to assess the relative strength of

163    10 competing generalized linear models (GLMs) that included different combinations of

164    predictor variables (Burnham and Anderson 2002; Appendix S1: Table S2). Specifically, we

165    evaluated the fit of a full model (M1) that included an interactive effect of habitat degradation

166    and edge proximity on the odds that tethered fauna would be consumed, as well as effects of

167    shoot density, epibiont biomass, and crustacean biomass. We compared this model to simpler

168    models that excluded one or more continuous variables (M2 – M6), a model that removed the

169    interaction between habitat degradation and edge proximity (M7), and models with only edge

170    proximity (M8) or habitat degradation (M9) as factors. To test for overall significance, we

171    compared all models to a null model with no predictors (M10). We compared models using

172    Akaike's Information Criterion corrected for sample size bias (AICc), delta-AICc (a measure of

173    the strength of evidence of each model relative to the best model, which has the lowest AICc

174    value: $\Delta i = AICc,i – AICc,min$), and AIC weights ($w_i$, the probability that model i is the best

175    fitting model). We ranked models at each site using $\Delta i$ and $w_i$ and considered $\Delta i < 2$ to indicate

176    substantial model support (Burnham and Anderson 2002). Using the output from the models with

177    strong support, we calculated odds ratios and 95% confidence intervals (CIs) to assess predation

178    risk effect size and variability for predictors. Odds ratios specify how the odds of being

179    consumed change when comparing one treatment to another (e.g., the odds of being consumed in

180    50% shoot loss plots vs. ambient plots, or at the edge vs. the interior), or how the odds of being

181    consumed change with a unit change in a continuous predictor variable (e.g., for each additional

182    gram of crustacean biomass). We treated CIs as "compatibility intervals" (sensu Amrhein et al.

183    2019) when judging the strength of treatment effects (see also Burnham and Anderson 2014).

184    Continuous variables were $\log_{10}$ transformed to improve normality, and data were pooled among

185    trials before analyses.

186         *Variability in edge effect strength among sites.* We next evaluated what factors explain

187    differences among sites in the strength of edge effects on predation risk (hereafter "edge effect

188    strength"). Specifically, we asked whether edge effect strength is correlated with edge-vs.-

189    interior differences in shoot density, epibiont biomass, and crustacean biomass among sites, and

190    whether the significance of these relationships depends on the level of habitat degradation. For

191    each level of habitat degradation at each site, we (i) used edge-vs.-interior odds ratios for

192    predation risk, generated from site-level GLMs described above, to represent edge effect

193    strength; and (ii) generated an edge-to-interior effect size for shoot density, epibiont biomass,

194    and crustacean biomass by calculating the log response ratio (LRR) for each variable. The LRR

195    is a dimensionless measure of effect size calculated by taking the natural log of the ratio of two

196    means, and is widely used as a measure of effect size for measurements on a physical scale

197    (Hedges et al. 1999). We then used linear mixed-effect models (with site as a random term) to

198    test whether the edge effect strength depends on edge-vs.-interior effect sizes for shoot density,

199    epibiont biomass, and crustacean biomass, and their interactions with habitat degradation.

200    Specifically, we used AIC, $\Delta$i, and $w_i$ to evaluate the fit of eight competing models (i.e., a full

201    model involving all two-way interactions which was subsequently simplified by removing terms,

202    and a null model; Table 1). We also tested models that included ocean basin (Atlantic and

203    Mediterranean vs. Pacific), taxon (shrimp vs. crab), and size of tethered organisms as factors, but

204    models including these factors had substantially worse model fits, and visualization indicated no

205    effects of these factors on edge effect strength. Thus, these factors were not considered further.

206    Our initial models included latitude as an explanatory factor, but its inclusion raised model AIC

207        values, and as a single factor latitude was not a strong predictor of edge effect strength ($r^2 = 0.04$,

208        $P = 0.15$). Latitude therefore was not included in final models. We visually assessed data for

209        normality and homogeneity of variance, and determined that edge-vs.-interior effect size for

210        shoot density, epibiont biomass, and crustacean biomass were not correlated with one another

211        before running tests (Pearson correlations: all r values < 0.3).

212        *Variability in habitat degradation effect strength among sites.* Lastly, we asked what

213        factors explain differences among sites in the strength of habitat degradation effects on predation

214        risk. Specifically, we tested whether habitat degradation effects on predation risk among sites are

215        correlated with the size of the effect of habitat degradation on crustacean biomass and on

216        epiphyte biomass, and with ambient shoot density at each site. In two separate analyses, we used

217        a response variable defined by the odds ratio of predation risk between ambient plots and those

218        with each level of degradation. Accordingly, we included as predictor variables the log response

219        ratios of crustacean biomass and epiphyte biomass between ambient plots and those with each

220        level of degradation, as well as ambient shoot density. We used AICc, $\Delta$i, and $w_i$ as described

221        above to compare the full model to simplified models and a null model. Initial models including

222        ocean basin, taxon, and organism size as factors provided poor fits to the data and thus were not

223        considered further.

224        All analyses were performed using the MASS, lme4, and MuMin packages in R version

225        3.5.2 (R core team 2018) and scripts are available at https://github.com/kahovel/Code.

226        **4. Results**

227        *Predation risk within sites.* Models M1 – M5, which included shoot density, epibiont

228        biomass, and crustacean biomass within the plot as predictors, had extremely poor fits at all 17

229        sites (all $w_i$ < 1%). M6, which included an interactive effect of habitat degradation and edge

230     proximity, also fit poorly at all sites (all $w_i$ < 3%). This leads to two important conclusions: first,

231     shoot density, epibiont biomass, and prey biomass had few direct effects on predation risk; and

232     second, habitat degradation did not affect relative predation risk along the patch edge compared

233     to the patch interior.

234         Overall, proximity to the edge of the seagrass patch was the most influential predictor for

235     predation risk (Appendix S1: Figure S2). M8, in which proximity to the edge was the only

236     predictor variable, was the best fitting model at seven sites, had substantial support ($\Delta$i < 2) at all

237     but one site (Mexico), and had the highest average support of all models ($\bar{x}$ $w_i$ = 42.7% $\pm$ 6.8

238     SE). The null model (M10) was the best fitting model at seven sites ($\bar{x}$ $w_i$ = 27.1% $\pm$ 5.0),

239     however, a competing model (M7, M8, or M9) also had substantial support at all but one of these

240     sites (Mexico). Habitat degradation had relatively little influence on predation risk. M7 and M9,

241     both of which included habitat degradation as a predictor, had substantial support at six sites, but

242     were the best fitting model at only one (Korea B) and two (France and Virginia) sites,

243     respectively, and had low support overall ($\bar{x}$ $w_i$ = 13.4% $\pm$ 3.1 and 15.4% $\pm$ 4.2 for M7 and M9,

244     respectively).

245         Focusing on individual sites, we also found significant edge effects on predation risk (i.e.,

246     CIs for point estimates did not overlap a value of one) at 10 out of 17 sites, and edges were less

247     risky than patch interiors for tethered prey at most of these sites (Figure 2). Predation risk was on

248     average 2.4 times higher in the patch interior than along the patch edge at Bodega Bay, Finland,

249     France, Korea B, Northern Ireland, San Diego, and San Francisco, but was on average 2.04 times

250     higher along the edge than in the patch interior at Japan North, Japan South, and Quebec (Figure

251     2). Point estimates suggested that predation risk also was higher in the patch interior than along

252     the edge in Oregon, Korea A, and Virginia, and higher along the edge than in the patch interior at

253    Croatia, though CIs at these sites overlapped a value of one, so we were unable to distinguish

254    whether edges increased, decreased, or did not strongly affect predation risk. At the remaining

255    three sites (Mexico, North Carolina, and Washington), point estimates were very close to a value

256    of one, suggesting negligible effects of edges on predation risk.

257         Overall we found small or variable effects of habitat degradation on predation risk,

258    corroborating results of model comparisons. In the 50% habitat degradation treatment, CIs

259    overlapped a value of one at all but the two sites in Korea, suggesting that at most sites, habitat

260    degradation could increase, decrease, or have no effect on predation risk (Figure 2). At Korea A

261    and B, the odds of being eaten were 140% higher in ambient plots compared to 50% habitat

262    removal plots. Point estimates for the 80% habitat degradation treatment suggested an increase in

263    predation risk with degradation at 11 out of 16 sites (in North Carolina there were not enough

264    organisms remaining alive to calculate odds ratios for habitat degradation). However effect sizes

265    varied widely among sites (range 3% to 291% increase in odds of being consumed) and all CIs

266    for odds ratios overlapped a value of one.

267         The effects of edge proximity on eelgrass shoot density, epibiont biomass, and crustacean

268    biomass were highly variable in strength and direction among sites (Appendix S1: Figure S3).

269    Thus, habitat features that may influence predation risk commonly covary with edge proximity,

270    but in different ways among sites.

271         *Variability in edge effect strength among sites*. The best fitting model explaining edge

272    effect strength ($w_i = 54.5\%$; $F_{7,40} = 4.5$, $P < 0.001$, $r^2 = 0.44$) was the full model that included (i)

273    habitat degradation, (ii) an interactive effect of habitat degradation and edge-vs.-interior effect

274    size for crustacean biomass, and (iii) edge-vs.-interior effect sizes for shoot density and for

275    epiphyte biomass (Figure 3; Appendix S1: Table S2). Of these terms, edge-vs.-interior effect size

276  for shoot density explained the highest proportion of the variance in edge effect strength:

277  predation risk was higher at patch edges (compared to patch interiors) at sites with lower shoot

278  density along patch edges. Additionally, in the ambient treatment (no habitat degradation), sites

279  with lower levels of crustacean biomass at patch edges had elevated predation risk at patch

280  edges. This effect was not present in the 50% or 80% habitat degradation treatments. Edge effect

281  strength also decreased with edge-vs.-interior effect size for epibiont biomass, though this term

282  explained a smaller proportion of the variability than other terms. There was a weak trend for

283  edge effect strength to increase with habitat degradation: on average, patch interiors were slightly

284  riskier than patch edges in ambient plots, but this trend was not present in degraded plots.

285      *Variability in habitat degradation effect strength among sites.* Variability in the effect of

286  habitat degradation on predation risk among sites was not explained by differences in crustacean

287  biomass or epiphyte biomass among treatments, or by ambient shoot densities at sites. The null

288  model was the best fitting model for predation risk at both 50% and 80% degradation relative to

289  ambient, and no competing models had strong support (Appendix S1: Table S3).

290

291  **5. Discussion**

292      Accelerating degradation and fragmentation of coastal marine habitats makes it

293  imperative to determine how changing habitat structure and configuration influence ecological

294  processes, and by what mechanisms. Provision of refuge from predation is a chief ecosystem

295  function of vegetated aquatic habitats. We tested for interactive effects of experimental habitat

296  degradation (loss of structural complexity) and patch edge proximity on epifaunal predation risk

297  in eelgrass communities at 17 sites spread across the Atlantic and Pacific oceans and

298  Mediterranean Sea. We found that proximity to the edge of a seagrass patch had larger effects on

299    predation risk than did habitat degradation within patches, and that habitat degradation did not

300    alter effects of edge proximity on predation risk. Edge effects varied in strength and direction

301    among sites, but edges were less risky than patch interiors for fauna at most sites. Among sites,

302    riskier edges tended to be those with low shoot density and epibiont biomass, and (in non-

303    degraded conditions) low crustacean biomass compared to patch interiors. This suggests an

304    indirect component to edge effects in which the impact of edge proximity on predation risk is

305    mediated by the effect of edges on key biotic factors: i.e., because the effect of edges on biotic

306    factors varies among sites, so too does the effect of edges on predation risk.

307        Our results contrast with research showing that patch edges have elevated predation risk

308    compared to patch interiors, including many studies in seagrass habitat that found elevated

309    mortality rates for prey along patch edges relative to patch interiors (e.g., Irlandi et al. 1995,

310    Bologna and Heck 1999, Gorman et al. 2009, Smith et al. 2011, Carroll et al. 2012, Mahoney et

311    al. 2018). However, our results are in accordance with recent syntheses and empirical results

312    suggesting that edge effects vary widely in direction and magnitude, even within the same

313    habitat type, both on land (Debinski and Holt 2000, Lahti 2001, Ries et al. 2004) and in the sea

314    (Boström et al. 2006, Selgrath et al. 2007, Carroll et al. 2012). Several factors may contribute to

315    this variability by influencing the density, behavior, or efficiency of predators, though these

316    factors have rarely been tested (Ruffell et al. 2014). These include differences in the structural

317    and spatial characteristics of habitats (i.e. landscape or seascape context: e.g. Donovan et al.

318    1997), the degree of contrast between two adjacent habitats (i.e. edge type), and time since edge

319    creation (Gieselman et al. 2013, reviewed by Harper et al. 2005). Edge effect strength and

320    direction also may depend on the degree to which biotic and abiotic factors differ between patch

321    edges and interiors. These indirect effects of edges occur when habitat features, or disturbances

322    to habitat, vary with proximity to an edge and dictate the strength of interactions occurring

323    within the patch (Ruffell and Didham 2016). For instance, vegetation structure increased with

324    distance from the edge of Australian forest patches, which in turn increased the abundance of

325    invasive ship rats (*Rattus rattus*) that prey upon on bird nestlings, and this effect was mediated

326    by the amount of disturbance by grazing cattle (Ruffell et al. 2014). Indirect effects of edges

327    likely are widespread, though they are seldom studied, in part because quantifying indirect

328    effects by experimentally controlling for factors such as habitat structure or prey density is

329    intractable in many habitat types (but see Macreadie et al. 2010, Villaseñor et al. 2015).

330    Additionally, most studies on edge effects do not take place over large enough spatial scales to

331    encompass the biogeographic variability in habitat features needed to address indirect

332    mechanisms.

333          The strength of edge effects on predation risk was highly variable across the range of

334    eelgrass in our study, and this variability was partly explained by variation in the physical and

335    community structure of the patch edge. Specifically, compared with patch interiors, edges with

336    low shoot density and low crustacean biomass tended to have higher predation risk. Increasing

337    structural complexity commonly reduces faunal predation risk because structural elements of

338    habitat can interfere with predator search and capture (Heck and Crowder 1991, Kovalenko et al.

339    2012). In particular, dense eelgrass may restrict the movement and field-of-view for predators

340    (Bartholomew et al. 2000), and epibionts that colonize seagrass shoots, particularly filamentous

341    algae, may contribute to lower predator detection of prey (Hovel et al. 2016). Together, shoot

342    density and epibiont biomass contributed to a large fraction of the variability in edge effect

343    strength among sites in our study. The fact that edges containing higher crustacean biomass than

344    patch interiors tended to have lower predation risk may reflect lower predator abundance along

345    edges, or alternatively, increasing crustacean biomass may decrease per capita predation risk by

346    diluting risk among individuals (Mattila et al. 2008).

347         Our results suggest that differences in structural complexity between patch edge and

348    interior, and perhaps crustacean biomass, contributed to the strength and direction of edge effects

349    on predation risk. But edges also can more directly influence predation risk by influencing

350    predator habitat selection and predator-prey encounter rates. Recent censuses of fish

351    communities within seagrass habitat suggest that juvenile or adult fishes (common predators on

352    small fauna) often may be associated with more contiguous seagrass habitat that contains fewer

353    edges (Staveley et al. 2017, Yeager et al. 2016) or larger patches with lower edge to interior

354    ratios (Laurel et al. 2003). This corresponds to the overall trend for riskier patch interiors than

355    patch edges in our study. In San Diego, where predation risk was significantly higher in the patch

356    interior than along the edge, juvenile fishes of several species are abundant within eelgrass patch

357    interiors and have diets consisting largely of crustaceans (Moore and Hovel 2010). Sites with no

358    edge-vs.-interior differences in predation risk may be characterized by more uniform

359    distributions of dominant fishes across meadows, such as red drum (*Sciaenops ocellatus*) and

360    pinfish (*Lagodon rhomboides*) in North Carolina (Mahoney et al. 2018), or staghorn sculpin

361    (*Leptocottus armatus*) in Washington and Oregon (Hayduk et al. 2019, Ruesink et al. 2019).

362    Furthermore, the higher risk for epifauna along seagrass patch edges at some sites may be

363    explained by large predators using unvegetated areas as corridors that facilitate movement

364    through benthic seascapes (Irlandi et al. 1995), or moving to seagrass habitat from other habitats

365    to forage (Gorman et al. 2009, Smith et al. 2011). At our Japan South site, large fish predators

366    such as adult rockfish (*Sebastes* spp.) move from adjacent sand flats to vegetated habitats at night

367    to forage, and in doing so encounter prey first along patch edges (see Kinoshita et al. 2012).

368 Likewise, at Japan North, we observed large flatfishes such as cresthead flounder (*Pleuronectes*

369 *schrenki*) moving from deeper, adjacent sand flats to eelgrass beds to forage on tethered grass

370 shrimp.

371      An important finding from our study is that proximity to patch edges had stronger effects

372 on mortality risk than did habitat degradation: even though differences in structural complexity

373 between patch edges and interiors may have helped dictate the strength of edge effects, the

374 removal of 50 – 80% of seagrass above-ground structure had highly variable, but often small

375 effects on mortality risk at each site (Figure 2). This was surprising, as we expected strong and

376 consistent increases in predation risk with habitat degradation based on the idea that structurally

377 complex habitats provide refuge for fauna by reducing predator-prey encounter rates. How

378 changes to structural complexity affect prey risk ultimately depends on how these changes affect

379 predator behavior and distribution. For instance, degradation can reduce rather than increase

380 predator-prey encounter rates if predators avoid areas of low structural complexity, which may

381 occur if higher-order predators pose a risk to them (e.g., Micheli 1997, Mahoney et al. 2018).

382 Our finding that effects of degradation on predation risk can vary widely among sites, and can be

383 positive or negative, likely reflects the variability in the type and abundance of mid- and top-

384 level predators among sites. Alternatively, it is possible that our degraded plots were not large

385 enough to affect the behavior of some predators, given that plots were embedded within larger

386 eelgrass patches in which structural complexity remained unchanged. In previous studies,

387 however, manipulations of eelgrass structural complexity over much smaller spatial extents (e.g.

388 0.05 $m^2$; Hovel and Lipcius 2001) altered the outcome of predator-prey interactions in eelgrass

389 habitat.

390       We also found that habitat degradation had little influence on whether patch edges were

391    riskier than patch interiors at individual sites. Habitat degradation might be expected to reduce

392    edge-vs.-interior differences in predation risk if degradation has an overwhelming effect on

393    predator behavior and predator-prey encounter rates (if, for instance, predators are much more

394    efficient at finding prey within degraded patches, regardless of their proximity to an edge;

395    Mahoney et al. 2018). The only strong effect of habitat degradation that we found was that the

396    inverse correlation between edge effects on crustacean biomass and the strength of edge effects

397    on predation risk disappeared when eelgrass was degraded. We did not observe reduced

398    variability in edge effect size for crustacean biomass in degraded plots, suggesting the alternative

399    explanation that habitat degradation may have led to edge-to-interior differences in the type or

400    behavior of alternative prey available in plots, or the type or behavior of predators that entered

401    plots in search of prey.

402       Several caveats apply to our findings. First, our experiments were conducted during a

403    narrow window of time in the summer, when eelgrass generally reaches peak biomass and shoot

404    length. However, eelgrass structural complexity and seascape structure can change seasonally,

405    particularly in southern locations that typically undergo above-ground defoliation when water

406    temperatures peak in late summer, and this can alter seagrass effects on predator-prey

407    relationships (Hovel and Lipcius 2002). For instance, in North Carolina, seasonal increases in

408    water temperature increased crab relative mortality in continuous seagrass but not in fragmented

409    seagrass, though edge effects on crab relative mortality were unchanged (Yarnall and Fodrie

410    2020). Thus, our findings may have differed if we had performed our experiments at other times

411    of the year. Second, we tested for edge effects on predation risk by making edge-vs.-interior

412    comparisons, rather than using a continuum of distances from seagrass patch edges. However,

413    our approach is appropriate for eelgrass habitat because the distance to which edge effects

414    penetrate into seagrass habitat often is very small (< 1 m: Tanner 2005, Macreadie et al. 2010).

415    Third, we did not standardize tethered prey among sites because our goal was to determine how

416    edge proximity affects predation risk for relevant mesopredators across the Northern

417    Hemisphere. Though the species we selected for tethering all are common prey items for higher-

418    order predators, using standardized prey may have resulted in more similar effects of edges and

419    habitat degradation on predation risk among sites. Finally, we were able to examine only a small

420    number of potential causes of variability in edge effects and predation risk. Patterns were

421    markedly different among our sites, and we were not able to explain the causes of much of this

422    variability. For instance, despite careful selection of similar eelgrass patches and edges among

423    sites, many aspects of seascape structure (e.g. nearest neighbor distance and seascape

424    composition) and related factors (e.g. hydrodynamic activity, which influences patchiness)

425    varied from site to site, which may have influenced the type and behavior of predators attacking

426    our tethered prey (see also Yeager et al. 2012, 2016). Future seascape-scale studies would benefit

427    from explicitly considering factors that covary with edge proximity and patchiness. In particular,

428    there is a need for more information on how biotic and abiotic covariates of edge proximity (e.g.

429    animal abundance, different components of structural complexity, and disturbances by

430    hydrodynamic activity and other factors) influence distribution and behavior of a range of

431    predator and prey species and associated organisms within food webs.

432    In conclusion, our results provide evidence that the effects of habitat patch edges on

433    faunal predation risk can vary widely in direction and strength, and suggest that structural

434    complexity of the patch edge may play a large role in determining how edges alter predator-prey

435    relationships. Determining how factors like patch edges and habitat degradation affect faunal

436  predation risk is important not only to better understand the consequences of habitat alteration on

437  population dynamics and ecological interactions, but also due to increasing evidence that top-

438  down processes directly affect the health and persistence of seagrasses (Whalen et al. 2013,

439  Reynolds et al. 2014) and other coastal habitats such as coral reefs (Mumby et al. 2006).

440  Strategies for restoring degraded seagrass habitat may differ depending on whether ecosystem

441  services (nursery habitat provision, carbon and contaminant sequestration, enhanced secondary

442  production, shoreline protection, and others) are more closely tied to edge proximity or to

443  structural complexity, or to other factors. Thus, determining the interplay of factors that control

444  predation risk for fauna, particularly in degraded conditions that are increasingly common in

445  seagrasses, is a key step in sustaining the suite of ecosystem services these habitats provide.

446

454  **7. References**

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616

617 Table 1. Predictors included in each of the ten candidate models for predation risk evaluated at

618 each site. Shoot density, epibiont biomass, and crustacean biomass all were $\log_{10}$ transformed for

619 analysis.

| Model | Predictors |
|---|---|
| 1 | Edge proximity * habitat degradation + shoot density +  epibiont biomass + crustacean biomass |
| 2 | Edge proximity * habitat degradation + shoot density + crustacean biomass |
| 3 | Edge proximity * habitat degradation + shoot density |
| 4 | Edge proximity * habitat degradation + crustacean biomass |
| 5 | Edge proximity * habitat degradation + epibiont biomass |
| 6 | Edge proximity * habitat degradation |
| 7 | Edge proximity + habitat degradation |
| 8 | Edge proximity |
| 9 | Habitat degradation |
| 10 | Null model |

620

621

Figure 1

**Figure 2**

Figure 3