Seaweed traits linked to wave exposure determine predator avoidance

Jeremy D. Long[1],*, L. Porturas[1], E. Jones[1], C. Kwan[1], G. C. Trussell[2]

[1]Department of Biology & Coastal Marine Institute Laboratory, San Diego State University, San Diego California 92182, USA
[2]Northeastern University Marine Science Center, Nahant, Massachusetts 01908, USA

ABSTRACT: Greater attention to habitat-specific species interactions should improve our ability to predict the context-dependency of species interactions. Predator avoidance depends upon resource traits that can vary predictably between habitats, but few studies have linked predator avoidance to habitat-specific resource traits. For example, predator avoidance in herbivores may depend upon wave exposure, because wave-exposed and wave-protected seaweeds display strong intraspecific differences in morphology and physiology that likely influence their value to herbivores. In 2 sets of laboratory mesocosm experiments we compared predator avoidance in the herbivorous snail *Littorina obtusata* offered the bladder wrack *Fucus vesiculosus* from either wave-exposed or protected shores. The effect of predation risk by the green crab *Carcinus maenas* on avoidance by *L. obtusata* depended on wave exposure, with a stronger effect of predation risk for snails on wave-exposed *F. vesiculosus*. To explore the traits responsible for this pattern, we conducted multi-choice feeding experiments with *F. vesiculosus* from 3 wave-exposed and 3 protected sites. *F. vesiculosus* from protected sites (where avoidance behaviors were weak) was more palatable than *F. vesiculosus* from wave-exposed sites. Although several morphological (e.g. blade width and vesicle number) and physiological traits (e.g. C:N ratio) of *F. vesiculosus* depended upon wave exposure, these were unrelated to snail feeding and predator avoidance. Therefore, *L. obtusata* displayed stronger predator avoidance on less palatable, wave-exposed seaweed. We suggest that the different effects of predators on rocky shores may partly reflect the influence of exposure-specific seaweed traits that determine predator avoidance.

KEY WORDS: Predation risk · Predator-prey interactions · Inducible defense · Non-consumptive effects

INTRODUCTION

The nonlethal effects of predators on prey should vary between habitats because of differences in refuge quality and quantity, prey and predator state, and predator and prey sensing (Grabowski 2004, Smee & Weissburg 2006, Heithaus et al. 2007, Trussell et al. 2008). For example, wave-exposure might weaken nonlethal effects because turbulence reduces prey perception of predators (Smee & Weissburg 2006). However, traits of algal or plant species that influence predator avoidance behaviors of herbivore prey may also differ between habitats. Two observations suggest a linkage between predator avoidance and habitat-specific plant or algal traits. (1) Prey may exhibit stronger predator avoidance when foraging on low quality foods because the attendant energy gains are not worth the risk (Brown & Kotler 2004). (2) Vascular plant or algal traits that determine food quality and herbivore foraging behavior often display predictable variation between habitats (e.g. Blanchette 1997). Thus, the strength of nonlethal effects of predators on herbivore prey may vary between habitats differing in plant or algal traits. Understanding this linkage may improve our ability to identify those habitats where nonlethal predator effects are most important to community structure.

A growing body of work has begun to document the effect of resource traits on predator avoidance. For example, on rocky shores, whelks seek refuge in response to predatory crab cues more often in the presence of barnacle versus mussel prey, perhaps because differences in the structural complexity provided by these resources change the degree of predation risk perceived by prey (Trussell et al. 2008). Similarly, a greater proportion of pea aphids vacate leaves after exposure to alarm pheromones when offered diluted (i.e. poor quality), as opposed to undiluted, artificial food solutions (Dill et al. 1990). Finally, caterpillar responses to predaceous stink-bugs depend upon tomato plant genotypes that vary in levels of chemical defense (Kaplan & Thaler 2010).

Although plant traits often vary predictably between habitats (e.g. shaded vs. non-shaded, Montgomery 2004; fellfield vs. snowbed, Shimono & Kudo 2003), it is unclear if such patterns can modify the nonlethal effects of predators on prey. For example, seaweeds display well-described intraspecific morphological variation as a function of wave exposure owing to the increased risk of dislodgement, enhanced mass transfer of nutrients, and reduced thermal stress typical of wave-exposed shores (Menge 1978, Blanchette 1997, Hurd 2000, Silva et al. 2010). In addition, wave-exposed seaweeds tend to have stronger holdfasts, narrower blades, shorter thalli, fewer air bladders, and lower C:N ratios compared to protected shore conspecifics (Knight & Parke 1950, Burrows & Lodge 1951, Armstrong 1987, Blanchette 1997, Edwards et al. 2006). These traits can strongly determine herbivore feeding preferences (Duffy & Paul 1992, Hay et al. 1994) and may, in turn, affect herbivore responses to predators. Therefore, the effect of predators may differ between wave-exposed and protected shores, in part because of differences in seaweed traits that determine avoidance responses in herbivores.

We performed 2 laboratory mesocosm experiments that compared predator avoidance of intertidal snails when offered seaweed from either wave-exposed or protected rocky shores. We also correlated avoidance behaviors with seaweed nutritional and morphological traits. Finally, we conducted multi-choice feeding experiments with these snails to compare the palatability of seaweed from wave-exposed and protected sites. Our goal was to compare the relative strength of

avoidance behaviors from these 2 habitat types and identify the traits likely responsible for habitat-specific avoidance behaviors.

MATERIALS AND METHODS

In 2 sets of experiments (2010 and 2011), we compared the avoidance behaviors of *Littorina obtusata* exposed to green crab *Carcinus maenas* risk cues while being restricted to *Fucus vesiculosus* from either wave-exposed along the S-SE-sides of Mount Desert Island, Maine, USA (Table 1). To determine the relative strength of wave exposure we used the cartographic exposure index, which ranges from 0 (extreme shelter) to 40 (extreme exposure). To calculate the cartographic index for our sites, we used GoogleEarth to count the number of 9° sectors radiating from each site with an open fetch ≥7.5 km (Rice & Kenchington 1990). The cartographic (mean ± SE) index was significantly greater at the wave-exposed (13 ± 2) than protected sites (2 ± 1; $t_{1,5} = 6.02$, p = 0.004). Although the maximum linear distance between sites was 13.8 km (OP to SH), we observed large differences in snail behavior when offered *Fucus* from close sites with different exposure (e.g. OP and OC are 1.4 km apart).

Because of taxonomic uncertainty within the *Fucus* genus (Hull et al. 2001, Villalard-Bohnsack 2003), we only collected *F. vesiculosus* thalli showing paired vesicles. Consistent with previous studies, vesicles were less common on wave-exposed *F. vesiculosus* (Knight & Parke 1950, Burrows & Lodge 1951). Hereafter, we simply use *Fucus* when referring to *F. vesiculosus*

Behavioral assays were conducted in replicate mesocosms (27 × 15 × 5 cm), each with an independent supply of seawater (~1 l min^{-1}) that flowed continuously into an upstream chamber, across a perforated barrier into a downstream chamber, and exited

Table 1. Collection sites for *Fucus vesiculosus* along the coast of Maine, USA. Wave exposure (Exp): e = exposed, p = protected

Site	Code	Exp	Latitude (N)	Longitude (W)
Bracy Cove	BC	p	44° 17′ 33″	68° 15′ 20″
Little Hunter's Head	LH	e	44° 17′ 54″	68° 12′ 27″
Otter Cove	OC	p	44° 19′ 00″	68° 11′ 60″
Otter Point	OP	e	44° 18′ 24″	68° 11′ 25″
Seawall	S	e	44° 14′ 31″	68° 17′ 56″
Seawall Point	SP	e	44° 14′ 10″	68° 18′ 02″
Ship Harbor	SH	p	44° 13′ 37″	68° 19′ 17″

through a mesh roof (see Trussell et al. 2006a for additional details). The upstream chamber (11 × 15 × 5 cm) was used to create 2 different predation-risk treatments (Risk vs. No Risk). A single green crab *Carcinus maenas* and 10 *Littorina obtusata* (to serve as food) were added to this chamber in Risk treatments. Eaten snails were replaced daily. No crabs were added to the No Risk treatments.

The flow rate (1 l min^{-1}) and downstream chamber volume (0.825 l) may have underestimated natural seawater flux, and therefore, exposed downstream snails to higher concentrations of crab cue (assuming that crab cue release is independent of flow). As with other similar mesocosm studies, this potentially limits the distances over which these cues are useful for snails. However, our emphasis here was to compare whether *Fucus* source influenced predator avoidance at any scale.

To the downstream chamber (16 × 15 × 5 cm), we added a single *Fucus thallus* (20 ± 1 g) and 10 intermediate-sized *Littorina obtusata*. In the 2010 experiment, *Fucus* was collected from one of 3 sites: 2 wave-exposed (OP or S) and 1 protected (BC). To more rigorously compare the influence of *Fucus* exposure history on snail behavior, we repeated the experiment in 2011 with better replication at the level of wave-exposure. Thus, the 2011 experiments used *Fucus* from 1 of 3 wave-exposed (OP, LH, or SP) or 3 protected sites (OC, BC, or SH). During both experiments (2010 and 2011), we crossed *Fucus* source with predation risk (Risk, No Risk) in a fully factorial design with 10 replicates per experimental combination. By repeating the experiment with *Fucus* from the same sites in 2010 and 2011 (OP and BC) we were able to explore temporal variation in these interactions. *Littorina obtusata* were collected from another protected shore that differed from the seaweed collection sites (Nahant; 42° 25′ 47″ N, 70° 55′ 34″ W). This is unlikely to be a confounding variable, as morphological responses of *L. obtusata* to green crab cues are similar from wave-exposed and protected shores (Trussell 1996). We selected juvenile snails because they display strong responses to green crab risk cues (Trussell et al. 2006a,b).

Because several studies have noted that *Littorina obtusata* avoid risky, profitable habitats and seek refuge when exposed to green crab cues (Palmer 1990, Trussell et al. 2008, Mowles et al. 2011), we characterized the avoidance behaviors of experimental snails in the downstream chambers by measuring the number of snails not residing on *Fucus* each day. Although such behaviors may temporarily increase predation risk, subsequent location of refuge habitats

can greatly reduce predation risk (see Kemppainen et al. 2005). In 2010, behavioral data were collected for 17 d with the exception of d 16 and as behaviors tended to be consistent across this longer period (Fig. 1), behavioral data were collected for only 5 d in 2011.

The 2010 experiment was designed to examine whether predator avoidance behaviors of *L. obtusata* varied by *Fucus* source. We calculated the mean daily avoidance of snails in each replicate (i.e. the average number of snails not residing on *Fucus*) and conducted an ANOVA with the average daily avoidance as the dependent variable, Risk (Risk, No Risk) as a fixed factor, and *Fucus* Source (OP, BC, and S) as a random factor. Because the 2010 experiment suggested that predator avoidance depended upon *Fucus* source, and that avoidance behaviors tended to be stronger on the wave-exposed shore *Fucus*, we designed the 2011 experiment to specifically examine whether Exposure (as opposed to site) interacted with Risk to influence snail behavior (i.e. average daily avoidance). Thus, for the 2011 experiment, we conducted a Nested ANOVA with Risk (Risk, No Risk) and Exposure (Exposed Shore, Protected Shore) as fixed factors, and *Fucus* Source as a random factor nested within Exposure.

Preliminary examination of 20 *Fucus vesiculosus* thalli from each of our 6 sites in 2011 suggested that wave-exposed and protected shore thalli differed in 4 morphological traits including blade length (cm, the length of blade-containing region of the longest
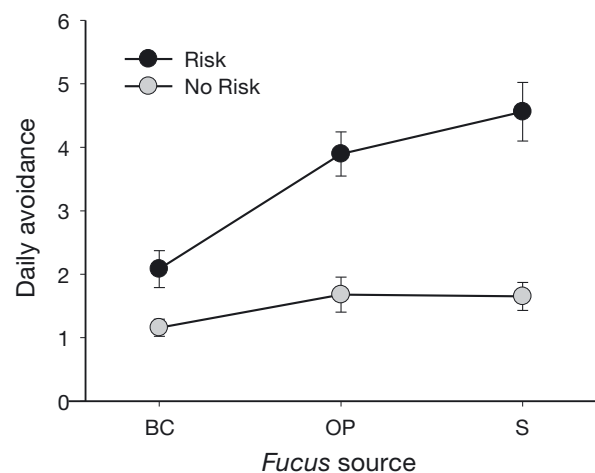

Fig. 1. Daily avoidance (mean ± SE) of *Littorina obtusata* under Risk and No Risk treatments when allowed to inhabit *Fucus vesiculosus* collected from 1 of 3 sites during 2010. Site codes see Table 1. Mean daily avoidance is defined as the number of snails not residing on *F. vesiculosus* and was calculated by averaging the replicates' average daily avoidance behaviors

branch), vesicle number (the number of vesicles on the longest branch), blade width (mm, the maximum blade width of a single branch), and midrib width (mm, the midrib width at the maximum blade width). Our preliminary observations agreed with previous reports about *Fucus* spp. morphology: protected shore *Fucus* possesses wider blades (Blanchette 1997, Ruuskanen et al. 1999) and more vesicles (Knight & Parke 1950, Burrows & Lodge 1951) than exposed ones. To examine if these morphological traits were associated with snail avoidance behavior, we measured all 4 traits for each of the 60 *F. vesiculosus* thalli (n = 10 for each of the 6 sites) in the Risk treatment used in the 2011 experiments. We conducted 2 types of analyses on these data. (1) We conducted 2-tailed, 2 sample *t*-tests to compare traits for wave-exposed vs. protected *Fucus*. We applied a Bonferroni correction to account for the multiple *t*-tests. (2) We explored the nature of the relationship between seaweed morphological parameters and predator avoidance behavior using a model selection approach. We expected that predator avoidance would be most influenced by blade width because wider blades potentially provide a greater predation refuge because of their increased area of attachment for snails. We fitted a linear model to our data and used Akaike information criterion to quantify the relative support the data gave for these models (Burnham & Anderson 2004).

To examine the influence of *Fucus* source on palatability, we conducted choice feeding assays with *Littorina obtusata*. In 2010, we examined the relative palatability of *Fucus vesiculosus* from a protected (BC) and a wave-exposed (S) site, respectively. Furthermore, to assess tissue-specific differences in palatability, the 2010 assays compared the palatability of either apical tip tissues or mid-blade tissues from the 2 sites. To examine the generality of our results from 2010 and to increase the number of sites in our comparison, we examined the relative palatability of *F. vesiculosus* from 3 protected (OC, BC, and SH) and 3 wave-exposed sites (OP, LH, and S) in a 6 choice feeding assay in 2011. Because 2010 assays suggested that sites differed primarily in the palatability of mid-blade tissues, the 2011 experiments only compared feeding on these tissues and avoided using seaweed segments having vesicles.

By offering snails a choice between protected and wave-exposed *F. vesiculosus*, our assays asked about the relative palatability of seaweeds from sites with different exposure — a factor that can influence herbivore foraging decisions. Because *L. obtusata* are unlikely to move between protected and wave-

exposed sites, our feeding assays did not represent realistic situations that individual snails encounter. Rather, these assays use herbivore preferences to provide insight into the relative palatability of seaweed from protected and wave-exposed sites. Palatability was emphasized because it measures the sum response of herbivores to multiple algal traits.

For all feeding assays, we measured the decrease in seaweed wet mass in replicates having snails (2010, n = 25; 2011, n = 30) after correcting for autogenic growth in snail-free controls (2010, n = 10; 2011, n = 30 randomly paired controls). Prior to assays, seaweed were blotted dry, cut to 0.4 or 0.3 g pieces (2010 and 2011, respectively), and placed in perforated replicate containers in tanks, each containing 5 *L. obtusata*. The remains of these thalli were bottled and recorded 3 d later. We calculated consumption using the formula $T_i(C_f/C_i) - T_f$, where T_i and T_f represent seaweed exposed to grazing, and C_i and C_f represent the control seaweed before (i) and after (f) the trial period. We compared the mean consumption of *F. vesiculosus* from different sites using 2-tailed, paired *t*-tests (2 choice assays for both tissue types in 2010) or the nonparametric Friedman's rank test (>2 choices, 2011). In 2011, post-hoc analyses of consumption rates were conducted with nonparametric multiple comparisons.

Because wave exposure can influence seaweed nutrient content, we measured carbon and nitrogen content of *Fucus* tissues using a Costech 1030 elemental analyzer and then calculated C:N ratios. These analyses were conducted on mid-blade tissues collected from the 3 sites in 2010 only (OP, BC, and S; n = 10). We conducted an ANOVA to examine the effects of *Fucus* source on C:N ratio.

RESULTS

In 2010, the effect of predation risk on mean daily avoidance behavior depended on *Fucus* source (Fig. 1, Risk × *Fucus* Source interaction, $F_{2,54} = 5.380$, p = 0.007). Although there was not a significant main effect of *Fucus* Source ($F_{2,54} = 2.345$, p = 0.299), there was a significant effect of Risk at α = 0.10 ($F_{1,54} = 11.783$, p = 0.075). For snails feeding on wave-exposed shore *Fucus* (OP and S), the effect of predation risk was much stronger than it was for snails feeding on protected shore *Fucus* (BC). In the presence versus absence of risk, 154% more snails displayed avoidance on wave-exposed *F. vesiculosus* whereas only 80% more displayed such avoidance on protected *F. vesiculosus*. In general, the number

of snails moving off *Fucus* increased during the first 5 d but then remained consistent for the remaining 12 d of the experiment.·

Similarly, in 2011 the effect of predation risk on average daily avoidance behavior depended on Exposure (Fig. 2, Risk × Exposure interaction, $F_{1,4}$ = 15.520, p = 0.017; see Table 2 for full analysis), with a stronger effect of predation risk on avoidance behavior for snails on wave-exposed shore *Fucus*. There were significant effects of Exposure (Fig. 3, $F_{1,4}$ = 13.214, p = 0.022) and Risk (Fig. 2, $F_{1,4}$ = 67.778, p = 0.001). Neither *Fucus* source nested within Exposure ($F_{4,4}$ = 4.460, p = 0.088) nor the interaction of *Fucus* source and Risk nested within Exposure ($F_{4,108}$ = 0.651, p = 0.627) significantly influenced snail behavior. In the presence of risk cues, an additional 2.1, 1.3, and 1.4 snails displayed avoidance behaviors on wave-exposed *Fucus* (OP, LH, and SP, respectively), but only an additional 0.8, 0.4, and 0.6 snails displayed avoidance behaviors on protected *Fucus* (OC, BC, and SH, respectively). In the presence versus absence of risk, 179% more snails displayed avoidance on wave-exposed *Fucus* whereas only 139% more displayed such avoidance on protected *Fucus*.

Consistent with our preliminary observations, wave-exposed and protected *Fucus* used in the 2011 avoidance experiment displayed unique morphologies (all means ± SE). *F. vesiculosus* from wave-exposed shores had narrower blades (11.6 ± 0.3 and 15.8 ± 0.4 mm, respectively; $t_{1,59}$ = 8.44, p < 0.001, Bonferroni corrected p < 0.05), fewer vesicles (3.5 ± 0.2 and 5.6 ± 0.3, respectively; $t_{1,59}$ = 5.71, p < 0.001, Bonferroni corrected p < 0.05), narrower midribs (2.9 ± 0.1 and 3.3 ± 0.1, respectively; $t_{1,59}$ = 2.67, p = 0.010, Bonferroni corrected p < 0.05), and longer blades (18.5 ± 0.6 and 16.0 ± 0.5, respectively; $t_{1,59}$ = 3.00, p = 0.004, Bonferroni corrected p < 0.05). However, the resulting low R^2 values indicated that individual morphological traits were poor predictors of mean daily avoidance behavior (blade width R^2 = 0.184, p < 0.001; number of vesicles R^2 = 0.172, p = 0.001; midrib width R^2 = 0.064, p = 0.029). Avoidance behavior did not depend upon blade length (R^2 = 0, p = 0.904). The linear regression containing *Fucus* blade width and number of vesicles as predictors of snail avoidance behaviors had the highest Akaike weight (0.45) and was more parsimonious than the next best model that contained 3 predictor variables instead of 2 (Table 3). Thus, blade width and number of vesicles best described the relationship between *Fucus* morphological traits and avoidance behaviors (Table 2; Number of snails displaying predator avoidance = 4.382−0.128 × blade width (mm) −0.192 ×
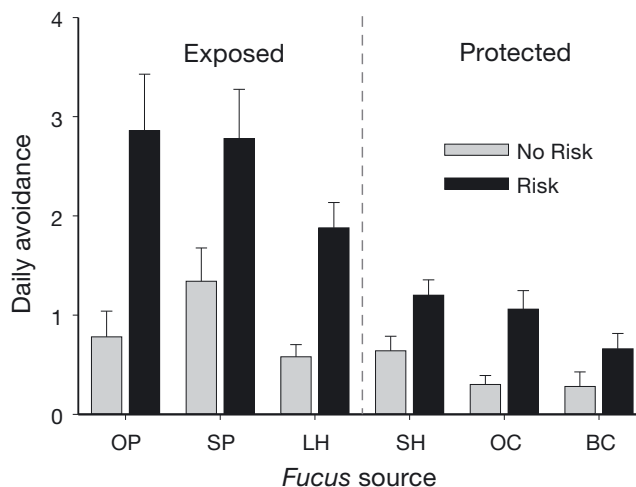

Fig. 2. Daily avoidance (mean + SE) of *Littorina obtusata* under Risk and No Risk treatments when allowed to inhabit *F. vesiculosus* collected from 1 of 6 sites during 2011. Mean daily avoidance is defined as the number of snails not residing on *Fucus*. Data are grouped by exposure of *Fucus* source

Table 2. Nested ANOVA testing the effect of wave exposure and risk stimuli on *Littorina obtusata* avoidance behavior during the 2011 experiment

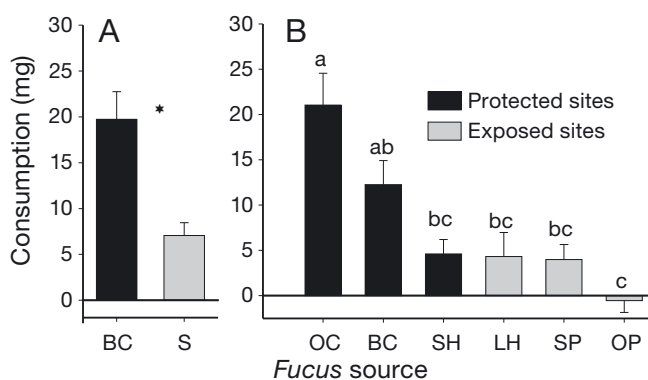| Source	df	MS	F	p
Exposure	1.4	30.805	13.214	0.022
Risk	1.4	35.425	67.778	0.001
Fucus source (Exposure)	4.4	2.331	4.460	0.088
Exposure × Risk	1.4	8.112	15.520	0.017
Risk × *Fucus* source (Exposure)	4.108	0.523	0.651	0.627

Fig. 3. Consumption (mean + SE) of mid-blade *Fucus vesiculosus* from protected and wave-exposed sites when offered to *Littorina obtusata* in feeding choice assays. Feeding assays were conducted with *F. vesiculosus* from either (A) 1 of each exposure type in 2010 or (B) 3 of each exposure type in 2011. Asterisk in (A) and letters in (B) indicate significant differences between groups. Difference in consumption was calculated using either a 2-tailed, paired *t*-test (A) or a Friedman's Rank Test (B)

Table 3. Models and the number of fitted parameters (k), the AIC$_c$ values, the difference in AIC$_c$ values used to predict predator avoidance behaviors, and the Akaike weight (w_i), which estimates the probability that a given model is the best model among those compared. The model with the smallest ΔAIC$_c$ is best supported by the data

Midrib width	No. of vesicles	Blade length	Blade width	AIC$_c$	ΔAIC$_c$	w_i
	×		×	21.47	0	0.46
	×	×	×	23.69	2.22	0.15
×	×		×	23.75	2.28	0.15
×	×			25.58	4.10	0.06
			×	25.82	4.35	0.05
×	×	×	×	26.07	4.60	0.05
	×			26.66	5.19	0.03
×	×	×		27.87	6.39	0.02
		×	×	28.02	6.54	0.02
×			×	28.03	6.56	0.02

number of vesicles; $F_{2,57} = 11.136$; p < 0.001). However, this model only explained 25.6% of the variance in average daily avoidance.

Littorina obtusata feeding depended upon *Fucus* source (Fig. 3). Mid-blade *Fucus* from BC (protected), was consumed 80% more than mid-blade *Fucus* from S (wave-exposed; $t_{1,24} = 4.547$, p < 0.001, Fig. 3A). In contrast, there was no significant difference in the palatability of apical tip tissues from the 2 sites, so palatability differences were tissue-specific (14.5 ± 2.3 mg and 12.0 ± 3.3 mg for BC and S, respectively; $t_{1,24} = 0.528$, p = 0.602). Although *L. obtusata* consume apical *F. vesiculosus* tissues, the damage caused by snail foraging is more common on mid-blade regions (J.D.L. and E.J. pers. obs.). In 2011, there was a trend for the 3 most preferred sources of mid-blade *Fucus* to be from protected sites (Fig. 3B). Interestingly, the most preferred *Fucus* (from the protected site OC), and the least preferred *Fucus* (from the wave-exposed site OP) were the 2 closest sites and separated by only 1.4 km.

While stronger avoidance responses and lower feeding preferences should be associated with foods with high C:N ratios, we observed the opposite pattern (i.e. stronger avoidance and lower feeding preference for low C:N ratios). For example, avoidance responses were higher on wave-exposed shore *Fucus* (OP, S; Fig. 1) and mid-blade regions of wave-exposed shore *F. vesiculosus* were preferred less in a choice feeding assay (Fig. 3). Yet, C:N of mid-blade regions varied significantly (ANOVA: $F_{2,27} = 48.46$, p < 0.0001) between 1 protected and 2 wave-exposed sites. *A priori* comparisons revealed that mid-blade

C:N (means ± SE) of wave-exposed *Fucus* from both OP (30.54 ± 0.47, mean ± SE) and S (30.01 ± 0.73, mean ± SE) was significantly lower (linear contrasts, p < 0.001, respectively) than that of protected *Fucus* from BC (34.06 ± 0.52, mean ± SE).

DISCUSSION

The source (wave-exposed vs. protected) of *Fucus vesiculosus* strongly influenced the strength of predator avoidance of snails encountering green crab risk cues while residing on those seaweeds. Strong avoidance responses of snails on wave-exposed shore *F. vesiculosus* were reduced simply by replacing the seaweed with a protected shore *F. vesiculosus thallus*. Thus, prey responses to predators were influenced by seaweed traits that varied predictably between habitats differing in wave exposure.

Our results support the increasingly important notion that species interactions are context-dependent (Bronstein 1994, Salomon et al. 2010, Grinath et al. 2012), and that habitat characteristics can be key to defining this context. Three examples highlight this finding. (1) The relative importance of predation by *Pisaster* sea stars can vary dramatically (from weak to keystone) between sites because of differences in prey production and sand deposition (Menge et al. 1994). (2) Switching from a diurnal to a mixed semidiurnal tidal regime can increase the trait-mediated indirect effects of predators on cordgrass production via changes in herbivore behavior (Kimbro 2012). (3) Elk vigilance to predation risk by wolves increases as elk move away from conifer forests and into open grasslands (Liley & Creel 2008). Identifying habitat traits that influence the behaviors of predators and prey will ultimately lead to a better understanding of the role of predators in structuring communities and influencing ecosystem function.

The stronger predator avoidance response of snails on wave-exposed *Fucus* may emerge because continued foraging on these less preferred seaweeds in the presence of predators is not worth the risk (sensu Brown & Kotler 2004). The results from our choice feeding experiment support this hypothesis: *Fucus* from wave-exposed sites (i.e. seaweed that created stronger avoidance behaviors) were less preferred than *Fucus* from protected shores. Because resource quality can vary predictably between habitats (e.g. with different elevation, sun exposure, etc.), avoidance behaviors may generally depend upon habitat-specific resource traits.

The habitat-specific avoidance behavior we observed may have been caused by risk-related shifts in herbivore physiological demands. In the presence of risk, herbivores may prefer foods that can rapidly fuel stress responses, such as foods with a greater proportion of digestible carbon. Grasshoppers shift their preference to artificial foods having higher ratios of digestible carbohydrates in the presence of spider risk cues (Hawlena & Schmitz 2010). If *Littorina obtusata* respond similarly to their predators, then avoidance responses may be weaker on protected shore *Fucus* with higher C:N ratios, in part, because these seaweeds better meet the energetic demands of stressed snail.

Although other *Fucus* traits differed between protected and wave-exposed shores, these do not appear to strongly influence snail feeding or predator avoidance behaviors. *Fucus* from wave-exposed shores had narrower blades, fewer vesicles, narrower midribs, and longer blades, but these traits accounted for <26% of the variation in predator avoidance behaviors.

Habitat-specific, predator avoidance of snails were consistent during Day 5 to 17 of our mesocosm experiments, suggesting that the seaweed traits driving snail behaviors were not plastic over these time periods. This might be expected because tissue damage caused by snails was concentrated on mid-blade tissues that lack plasticity once created (Long & Hamilton unpubl. data). Although seaweed morphology and chemical defenses can respond rapidly to environmental change (<1 m, Blanchette 1997, Toth & Pavia 2000, Long et al. 2007), plastic responses should be less common on mid-blade *Fucus* tissues because growth is apical and translocation is assumed to occur predominantly in a directional manner towards apical tissues (Diouris & Floc'h 1984).

Our experiments provide initial insight into a novel mechanism by which nonlethal effects may differ on protected and wave-exposed shores. A limitation of our design was the use of snails from protected sites only. We selected this design because we assumed that predators have the largest impact on protected shore snails. The design may have introduced bias because all snails had experience with protected shore *Fucus* and this familiarity could have influenced predator avoidance or feeding behavior. While additional experiments are needed to fully explore this hypothesis, we suspect that these patterns are not dependent upon snail source for 3 reasons. (1) Dietary history tends to have short-term effects (days) on herbivore behavior (Lyons & Scheibling

2007). Such effects should not have persisted across our avoidance behavior assays that lasted as many as 17 d.(2) The majority of studies that have examined the influence of dietary history on feeding preference indicate that herbivores tend to prefer unfamiliar foods, presumably as a means of diet mixing (Pennings et al. 1993, Poore & Hill 2006, Lyons & Scheibling 2007). This suggests that our observed preference of snails for protected shore *Fucus* would have been even stronger for wave-exposed snails. (3) Pilot studies have revealed that wave-exposed and protected snails display similar preference for *Fucus* grown without grazers relative to *Fucus* grown with grazers (J.D.L. pers. obs.).

The effect of crab predators on prey are often assumed to be stronger on protected vs. wave-exposed shores (e.g. Silva et al. 2010), perhaps because reduced turbulence on protected shores improves the ability of prey to detect chemicals released by actively hunting predators (Smee & Weissburg 2006). However, our study suggests that on a per-predator basis, there may be times when the nonconsumptive effects of crabs are stronger on wave-exposed shores. During calm periods on wave-exposed shores, the strength of nonconsumptive effects could increase because (1) the negative effect of wave-related turbulence on prey perception of predators is reduced, and (2) seaweed traits increase the strength of predator avoidance behaviors of prey. Alternatively, during other periods, increased turbulence could reduce the strength of nonconsumptive effects on wave-exposed shores as prey lose the ability to detect predators.

During calm periods, stronger nonconsumptive predator effects in wave-exposed seaweed communities could shift herbivore pressure and nutrient release (i.e. excretion) to alternate seaweed species or refuge habitats. In terrestrial communities, such habitat shifts can influence nutrient cycling via changes in nutrient content of herbivore tissues that alter microbial processes affecting carbon mineralization (Hawlena et al. 2012). Such a scenario is also possible in intertidal settings given the recent discovery that nutrient uptake by benthic seaweeds is influenced by intertidal herbivores (Bracken et al. 2011).

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