Foraging preference of whelks *Nucella lapillus* is robust to influences of wave exposure and predator cues

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ABSTRACT: In intertidal communities, abiotic factors like wave exposure can directly and indirectly affect an organism's morphology, foraging behavior, available prey, prey choice, and predators. Although these factors may be transient, their influences persist to affect optimal foraging decisions of intermediate consumers and any accompanying behaviorally mediated trophic cascades. In this study, we documented the influence of wave action on prey available to the whelk *Nucella lapillus* at wave-exposed and wave-protected sites in the Gulf of Maine. We then determined if whelks from wave-exposed and wave-protected sites similarly reduced foraging in response to cues from the predatory invasive crab *Carcinus maenas* and if crab cues altered the whelks' preference for barnacles *Semibalanus balanoides* over mussels *Mytilus edulis*. We found that while mussels were more abundant at wave-exposed sites than at wave-protected sites, whelks from both habitats consistently preferred barnacles and did not switch prey in the presence of crab cues. Furthermore, the influence of crab cues on the whelks' foraging was not detected in the consumption of the less preferred prey (mussels), and in the consumption of barnacles, it was only consistently observed in whelks taken from wave-protected sites. We suggest that the whelks' preference for barnacles over mussels demonstrates an optimal foraging decision in which the whelks are maximizing energetic gain by choosing the less energetically demanding prey. While local populations of whelks may express different behavioral responses to predators due to abiotic conditions, our results suggest that the preference of *N. lapillus* for barnacles is not altered by predator cues, wave exposure, or prior diet.

KEY WORDS: *Nucella lapillus* · *Carcinus maenas* · Mussel · Barnacle · Wave exposure · Predation risk · Prey choice · Indirect interaction

INTRODUCTION

Organisms in the intertidal zone must acclimate to extreme temporal and spatial variation in abiotic conditions like temperature, salinity, submergence, and wave action (Paine 1974, Menge 1976, Bertness 1981). In particular, wave action can strongly influence species composition in marine intertidal zones by impacting recruitment, nutrient availability, and predator abundance (Menge 1976, Robinson et al. 2011). On wave-exposed shores in the Gulf of Maine (GOM), increased thrashing, water flow, recruitment, and available nutrients favor hardy algae, small mus-

sels, and barnacles (Menge 1978, Etter 1996, Leonard 2000). Wave action further impacts species interactions by physically disrupting both the foraging ability of mobile predators (Menge 1978, Etter 1996, Robles 1997, Leonard 2000, Robinson et al. 2011) and the reliability of chemical cues they employ to locate prey (Weissburg & Zimmer-Faust 1993). Through a combination of these physical forcing mechanisms, predators in high-flow areas experience increased difficulty locating and handling prey (Etter 1996, Robles 1997, Robinson et al. 2011), and mussels and barnacles are relieved of the strong predation pressure they experience at low-flow sites

(Menge 1978, Leonard et al. 1998, Leonard 2000). Thus, factors associated with wave action establish the context of ecological interactions of intermediate intertidal consumers by affecting cue reliability and the distributions of higher trophic predators or lower trophic prey or by directly affecting consumer behavior and morphology.

Intermediate consumers can transmit the influence of predators to lower trophic levels through behavioral or morphological response to predators (non-consumptive effects [NCEs]) or through predation-related mortality (consumptive effects [CEs]). By eliciting 'fear' in any potential prey nearby, NCEs can have impacts on ecosystem structure equal to, or greater than, CEs (Schmitz et al. 2004, Trussell et al. 2004, Hernández & Laundré 2005, Matassa & Trussell 2011, but see Weissburg et al. 2014). For an intermediate consumer, predation threats and abiotic stresses (like wave action) often create similar trade-offs in fitness and/or optimal foraging; by attaining a refuge from either threat, an organism must forgo acquiring energy needed for growth and reproduction (Sih 1980, Burrows & Hughes 1991a, Schmitz et al. 2004). The intertidal carnivorous snail *Nucella lapillus* (also known as dog whelk and Atlantic dog-winkle; hereafter *Nucella*) is an important intertidal predator on mussels and barnacles and is in turn preyed on by several crab species. In the GOM, native rock crabs *Cancer irroratus* and *C. borealis* and the invasive European green crab *Carcinus maenas* are important predators of *Nucella* and elicit behavioral and morphological responses in several gastropods (Palmer 1990, Trussell et al. 2006, Smee & Weissburg 2008, Freeman & Hamer 2009, Large & Smee 2010, Matassa & Trussell 2011).

High wave exposure can influence *Nucella* morphology directly by favoring structures necessary for attachment to substrates (e.g. a larger pedal surface area and a larger aperture; Etter 1988) or indirectly by limiting predators to wave-protected sites, where *Nucella* produces better-defended phenotypes (thicker shells and smaller aperture areas relative to their shell lengths) than *Nucella* observed on wave-exposed shores (Kitching et al. 1966, Crothers 1985, Palmer 1990, Freeman & Hamer 2009). Moreover, *Nucella* from high-flow areas have reduced foraging efficiency and reduced morphological and/or behavioral responses to predators compared to protected-shore *Nucella* (Burrows & Hughes 1989, Etter 1996, Freeman & Hamer 2009, Robinson et al. 2011, Freeman et al. 2014). Because *Nucella* lays eggs that hatch as juvenile snails, the whelk can adapt to biotic and abiotic conditions both locally (Etter 1989, Bur-

rows & Hughes 1991b, Rovero et al. 1999) and across large geographic gradients (Crothers 1985, Sanford et al. 1994, Bertness et al. 1999, Large & Smee 2010, Freeman et al. 2014). Differences in available prey and community composition along a wave-exposure gradient may also influence *Nucella's* ecological interactions. Behavioral trophic cascades involving *Nucella* are stronger with preferred barnacle prey (Trussell et al. 2008). In addition, through experience or ingestive conditioning, some *Nucella* spp. retain preferences for prey species they consume *in situ* and increase foraging efficiency on those prey (Dunkin & Hughes 1984, Hughes & Dunkin 1984a,b, West 1986, Burrows & Hughes 1991b, Hughes et al. 1992, Rovero et al. 1999).

While experiments involving *Nucella* have revealed a good deal about NCEs, it is not known if whelks switch prey in response to predator cues or if all populations acclimate to different prior diets. While *Nucella's* specialization on barnacles is important for transmitting trophic cascades (Burrows & Hughes 1989, Trussell et al. 2008), it may also be influenced by alternative prey (e.g. West 1986, Burrows & Hughes 1991a). Other aspects of individual specialization can have large effects on food webs (Bolnick et al. 2003). The absence of specialization, or prey switching, may also have important effects on lower trophic levels, including stabilizing prey populations (Murdoch 1969) or destabilizing prey (Estes et al. 1998). By switching prey from pinnipeds to sea otters, orcas reduce predation on sea urchins, leading to overgrazing of many kelp forests in coastal Alaska (Estes et al. 1998). Even within such a trophic cascade, among-individual diversity of sea otter prey choice and foraging behavior adds variation to food web topology (Tinker et al. 2008). Prey switching may also propagate non-lethal trophic interactions (NCEs). The threat of tiger shark predation influences diving behaviors, habitat choices, and feeding behaviors of dugongs and sea turtles, leading to subsequent changes in seagrass communities (Heithaus et al. 2007, Burkholder et al. 2013).

In this study, we investigated the combined effects of wave exposure, available prey, and the presence of a predator (*Carcinus maenas*) on the prey choice of *N. lapillus.* If *Nucella* foraging decisions are determined by a combination of prior experience and perceived predation risk, we predicted that when barnacles and mussels are both available, *Nucella* from wave-exposed sites would consume a higher percentage of mussels than would *Nucella* from wave-protected sites (because exposed-shore *Nucella* encounter mussels *in situ*). We further predicted that

Nucella would switch to the safer prey option of barnacles in the presence of a crab. Barnacles are presumed to be safer, as they take less time to consume than mussels (Dunkin & Hughes 1984, Burrows & Hughes 1990), allowing whelks to return to refuge quickly, and since crabs also feed on mussels, *Nucella* would be more likely to encounter a crab while feeding on a mussel than on a barnacle.

MATERIALS AND METHODS

Wave exposure assessment

To compare wave action at exposed and protected mid-coastal Maine intertidal sites near the Darling Marine Center (DMC; Table 1) in 2013, we used *in situ* placement of clod cards (adapted from Thompson & Glenn 1994). Clod cards (see Dernbach 2014 for detailed methods) were deployed on horizontal rocky intertidal ledges by driving a stainless steel bolt through the steel mesh card and into predrilled holes in the rock. Dissolution (difference between initial and final weights) was analyzed using an ANOVA, with Site and Set designated as random factors and Wave Exposure (WE) designated as a fixed factor. A Tukey test was then used to compare dissolution between sites and wave exposures.

Intertidal species cover

To compare the sessile animal cover at wave-exposed and wave-protected sites, a 0.5 m² quadrat was placed on horizontal surfaces randomly along a 15 m transect line at wave-exposed and wave-protected sites. To help quantify cover, the reference quadrat was partitioned with string into 25 equal squares. The cover of barnacles, mussels, and bare rock was analyzed from 20 quadrats per site (10 from each exposure) using an ANOVA, with WE designated as a fixed factor and Site designated as a random factor. Because Site was designated as a random variable, the statistical program JMP used Site × WE to approximate the denominator mean squares and degrees of freedom when testing for the effect of WE.

Species collection

In 2012, *Nucella* were collected from 6 site pairs near the DMC (Table 1): 3 on the continuous coastal mainland (Kresge, Chamberlain, and Georgetown) and 3 on islands in the GOM, 2.5 to 19.5 km offshore (Thrumcap, Darmiscove, and Monhegan; Table 1). In 2013, we collected from 3 mainland site pairs: Kresge, Chamberlain, and Ocean Point. At each site, *Nucella* were collected from 10 random points along a 15 m transect line placed on a rocky intertidal shelf, parallel to the waterline during low tide about 1 m above mean low water. A 0.5 m² quadrat was placed at each point, and all the *Nucella* in each quadrat were collected. *Nucella* were immediately transported to flowing seawater tanks at the DMC and fed mussels every 2 to 4 d. Fresh *Nucella* were collected as needed from mainland sites using the same technique, but *Nucella* from island sites were not replenished (Table 1).

Barnacle-covered cobbles and granite tiles (in 2012 and 2013, respectively) were used as food sources to quantify changes in *Nucella's* foraging rates in response to predation threat. In 2012, cobbles (7.5 × 6.5 × 4.5 to 14 × 11 × 7.5 cm) on which *Semibalanus balanoides* had settled were collected from the intertidal zone of the Damariscotta River Estuary near the DMC. Excess barnacles were scraped off cobbles until each cobble had a similar number of individuals (37 to 55 barnacles per cobble). The barnacle-covered cobbles were kept in the flow-through tanks for 24 h prior to each trial. Experiments in 2013 capitalized on a successful recruitment of barnacles (*S. balanoides*) onto granite recruitment tiles. In February 2013, 60 granite tiles (15 × 15 × 1 cm) were deployed in the Damariscotta River Estuary off the DMC floating dock. Tiles were attached to vertical ropes 1 to 2 m below the DMC floating dock in

Table 1. Field collection sites for *Nucella* in 2012 and 2013. Pairs of wave-exposed and wave-protected shores within 150 m were selected at each site. Whelks (250 to 300 individuals) were collected at each site

Year	Date sampled	Site	Latitude N	Longitude W
2012	28 June	Monhegan Island	43° 45.908	69° 19.207
2012	27 June	Damariscove Island	43° 46.023	69° 36.725
2012	26 June	Georgetown	43° 46.373	69° 43.968
2012	27 June	Thrumcap Island	43° 49.188	69° 32.976
2012	24 June, 25 July	Kresge	43° 50.121	69° 30.873
2012	25 June, 25 July	Chamberlain	43° 53.057	69° 28.558
2013	11 June, 22 July	Ocean Point	43° 48.878	69° 35.562
2013	10 June, 24 July	Kresge	43° 50.121	69° 30.873
2013	10 June, 23 July	Chamberlain	43° 53.057	69° 28.558

pairs, with each tile's rough side facing out. Tiles were retrieved from the dock and scraped to remove excess barnacles (341 to 783 barnacles per tile). At 1 d prior to the start of each experiment, *Carcinus* crabs (carapace width 6.5 to 8.0 cm) were collected from the Damariscotta River Estuary intertidal zone.

Induced prey choice experiment

To determine how predator cues alter the feeding preferences of *Nucella* from different wave exposures, we conducted a modified prey choice experiment, comparing *Nucella's* consumption of mussels and barnacles with or without crab cues. Unfiltered seawater from the Damariscotta River Estuary was fed into 2 header tanks (19 l buckets) that drained through tubing into each individual mesocosm placed in seawater tables at the DMC (Fig. 1). In 2012, there were 12 total mesocosms, and in 2013, there were 6 total mesocosms. Similar flow was provided to each replicate by routing seawater first through an overhead manifold that then fed each replicate. To maintain similar flow conditions, the same apparatus was used in both years. Each mesocosm received approximately 3 to 4 l of seawater per minute. For each trial, whelks from a site pair (wave-exposed and wave-protected shores at each site) were randomly assigned to 2 mesocosms. One mesocosm was designated as a control (with no crab present), and the other was designated as a crab cue (with a wire container holding 1 to 2 *Carcinus maenas*). Each mesocosm housed 2 vexar cages (30.5 × 15 × 7.5 cm). One vexar cage contained 10 whelks from the wave-exposed shore of a site, and one cage con-tained 10 whelks from the wave-protected shore of the same site. Each vexar cage contained 2 granite tiles placed side by side (Fig. 1; in 2012, cobbles were used instead of granite tiles). Whelks were allowed to choose between 20 mussels (*Mytilus edulis*, 10 to 40 mm) attached to one of the tiles and a barnacle-covered tile (in 2012, a cobble was used instead of a tile). Haphazard selection of mussels from predetermined size ranges ensured that replicates in each trial had similar size ranges of mussels. Replicates in each trial also received a similar distribution of barnacles on tiles or cobbles. Each trial lasted 4 d. In 2013, barnacle tiles were used until they ran out after 3 trials. Cue crabs were fed 2 crushed mussels every other day during the experiment.

Digital images of barnacle-covered cobbles or tiles were taken before and after feeding trials and analyzed in ImageJ to determine the number and aperture size of barnacles consumed. In addition, the number of mussels dead and drilled was counted and their shell lengths measured. In 2012, 6 separate trials were carried out per site, and in 2013, 3 separate trials were carried out per site. Between trials, mesocosms were thoroughly scrubbed, rinsed with seawater, and then haphazardly assigned new treatments. We attempted to have each replicate contain 10 *Nucella*. However, 41 (of 160) replicates had fewer than 10 whelks because only 6 to 9 whelks per replicate were available (as our whelk supply depleted) or 1 to 6 whelks died or escaped; hence, the number of mussels and barnacles eaten was evaluated per *Nucella* per replicate. To convert prey consumed per *Nucella* into energetic units, the prey's total dry mass (mg) was estimated using regressions from Burrows & Hughes (1990; barnacles: $y = 0.0632x^{2.954}$, mussels:
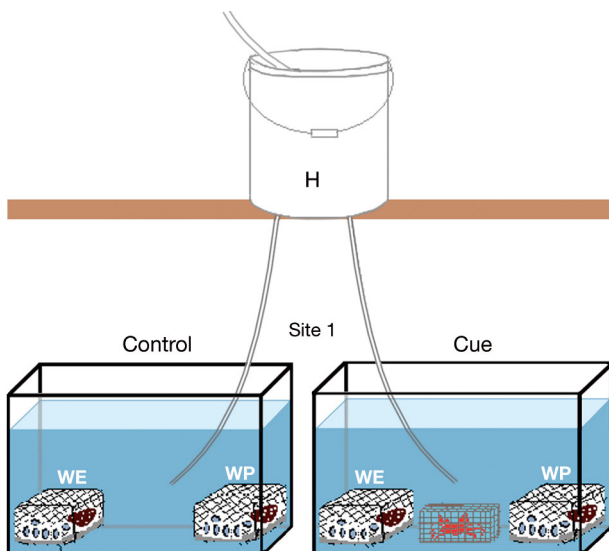

Fig. 1. Prey foraging experimental setup. To minimize flow variability, unfiltered seawater was poured into header tanks (H) and drained into each individual mesocosm below via identical pieces of tubing. Each site was randomly assigned to 2 mesocosms, designated as either control (with no crab present, left) or crab cue (with wire container holding 1 to 2 *Carcinus maenas,* right). A single mesocosm (58.4 × 41.2 × 31.4 cm) housed 2 rectangular vexar cages (30.5 × 15 × 7.5 cm). One cage held 10 whelks from the wave-exposed area (WE), and the other cage held 10 whelks from the wave-protected area (WP) from a single site (see text for details). Within each vexar cage, 2 granite tiles were placed side by side on the bottom. Twenty mussels were attached to one tile, and barnacle-covered cobble was placed on top of the other tile (in 2013, barnacle-covered tiles were used)

$y = 0.00901x^{2.851}$ where x = barnacle opercular length or mussel shell length, and y = dry mass). The dry mass was then converted to Joules consumed in each replicate: 23 J mg^{-1} for barnacles (Wu & Levings 1978) and 19.5 J mg^{-1} for mussels (Elner & Hughes 1978). Induced prey choice experiments were analyzed using a 3-way nested ANOVA in which both Trial and Site nested within WE were random variables. Initially, *Nucella* Shell Length was used as a covariate and Island as a fixed factor, but both were removed from the model because they were not significant (p > 0.11). WE and Cue, as well as their interactions, were designated as fixed effects. There was no significant interaction between the number of barnacles or mussels at the beginning of each trial and Site, WE, or Cue (indicating that initial prey densities did not affect consumption rates between trials). Higher-order interactions were removed from the model when they produced a p > 0.20. Analyses were carried out using the statistical program JMP 10 (SAS Institute).

RESULTS

Field site characterization

Analysis of clod card data indicated that wave-exposed sites generally had more dissolution than wave-protected sites, although there was site-to-site variation: Chamberlain showed the most dissolution for both exposed shore and protected shore (27.38 ± 1.02 and 11.21 ± 1.01 [least-squares mean ± SE], respectively), while Ocean Point showed the least for both exposed shore and protected shore (16.49 ± 1.02 and 8.66 ± 1.02; Fig. 2). While the interaction of Site and WE was significant (Table 2), post hoc comparisons indicate that at each site (except Kresge), the exposed shore had significantly higher dissolution than the protected shore (Fig. 2). Because of the poor resolution of plaster dissolution rates in mixed-flow environments (Porter et al. 2000), details of this post hoc comparison should be viewed with caution. In field surveys, post hoc comparison of WE × Site showed that, consistent with the findings of Leonard et al. (1998), there were more mussels on exposed shores than on protected shores (Fig. 3a; Table 3). The highest percent cover of mussels (11.22 ± 1.23) occurred at the most
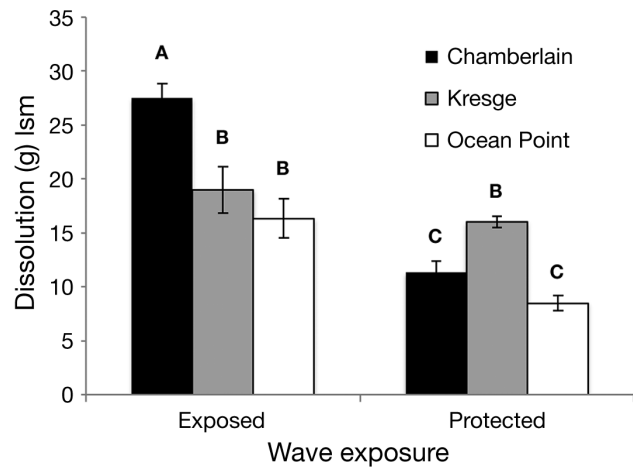

Fig. 2. Wave exposure assessment: dissolution (g) of clod cards deployed in the field in 2013 at each of the 3 sites (mean ± SE; see ANOVA results, Table 2). Bars with the same letter are not significantly different in post hoc Tukey test. lsm: least-squares mean

wave-exposed site, Chamberlain (Fig. 2). Barnacle cover was also significantly higher on exposed shores, but barnacles were still abundant at the protected sites (Fig. 3b). Conversely, protected shores had significantly more bare rock (Table 3, Fig. 3c).

Foraging experiment

An ANOVA of the number of barnacles consumed per *Nucella* indicated significant effects of WE, Cue, and Year (Fig. 4a, inset values; Table 4). Exposed-shore *Nucella* consumed fewer barnacles than protected-shore *Nucella* (wave-exposed = 2.78 ± 0.25 and wave-protected = 4.19 ± 0.25). *Nucella* experiencing crab cues consumed significantly fewer barnacles than those in the control tanks with no crab

Table 2. Wave exposure assessment: ANOVA results comparing the dissolution of clod cards at field sites in 2013 (Site = Kresge, Chamberlain, and Ocean Point). Wave Exposure (WE) consisted of wave-exposed and wave-protected shores. Set refers to clod cards made from the same batch of plaster and deployed at each site during the same tidal cycle. For this and remaining tables values in **bold** indicate significant difference (p < 0.05)

Source	df	Sum of squares	*F*-ratio	Prob > *F*
Set (Random)	1, 1	152.1	6.9847	0.2303
Site (Random)	2, 2	314.06	1.1799	0.4587
WE	1, 2.3659	729	4.9060	0.1372
Set × WE (Random)	1, 28	21.7778	3.4690	0.0731
Site × WE (Random)	2, 28	266.17	21.1991	**<0.0001***

a. Mussel cover

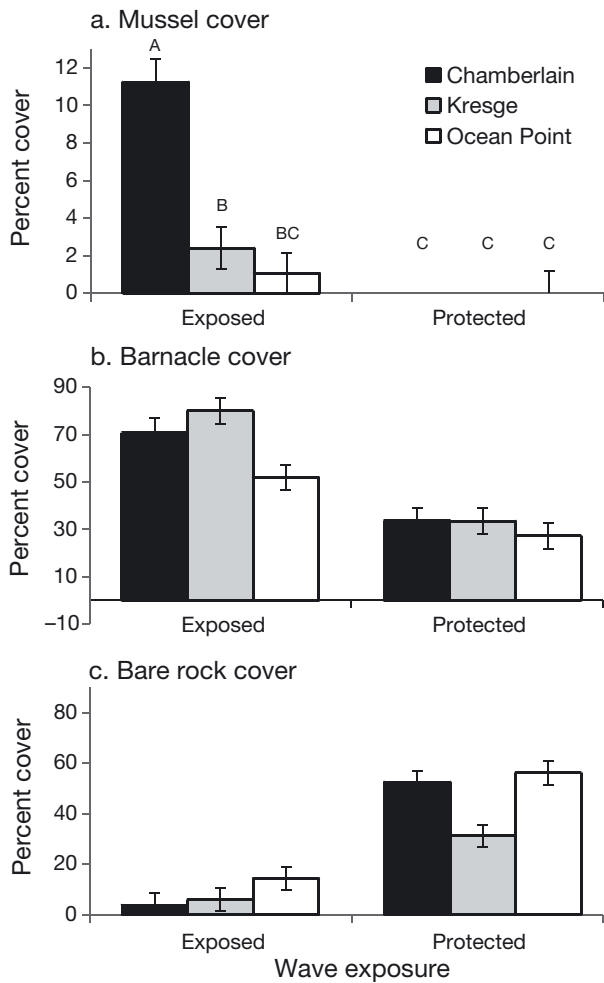## b. Barnacle cover

c. Bare rock cover

Fig. 3. Intertidal species cover: effect of wave exposure on the percent cover of (a) mussels, (b) barnacles, and (c) bare rock. Letters as in Fig. 2. ANOVAs were conducted on arcsine square root transformed cover values, but the figures were generated from ANOVAs of untransformed values

Table 3. Intertidal species cover: ANOVA of field surveys comparing the effect of wave exposure on the percent cover (arcsine square root transformed) of mussels, barnacles, and bare rock in 2013. In 2013, sites included Chamberlain, Kresge, and Ocean Point. Site and Wave Exposure (WE) as in Table 2

Source	df	F-ratio	Prob > F
Mussels			
Site (Random)	2, 2.0002	1.0000	0.5000
WE	1, 2	4.3048	0.1737
WE × Site (Random)	2, 51	18.6645	**<0.0001***
Barnacles			
Site (Random)	2, 2.0025	2.8686	0.2585
WE	1, 2	32.4173	**0.0284***
WE × Site (Random)	2, 51	1.8640	0.1655
Bare rock			
Site (Random)	2, 2.0016	2.1960	0.3129
WE	1, 2	32.2520	**0.0296***
WE × Site (Random)	2, 51	2.9862	0.0594

patterns in 2012 and 2013 suggest that food limitation did not affect *Nucella's* order of preferences; however, the preference for barnacles is likely to be conservative in 2012. An ANOVA of *Nucella's* energetic intake of barnacles indicated that in 2012, both wave-exposed and wave-protected whelks reduced foraging in response to crab cues, while only wave-protected whelks did so in 2013, and there was no overall difference between years (Fig. 4, Table 5). In contrast, *Nucella's* energetic intake of mussels did not change in response to crab cues or wave exposure but did decrease in 2013 (Fig. 4, Table 5).

Table 4. Prey foraging (ANOVA): barnacles and mussels consumed per *Nucella*. Cue consisted of crab (*Carcinus maenas*) or control (no predator). Wave Exposure (WE) as in Table 2. Site was included as random factor nested within WE. Because JMP uses the restricted maximum likelihood technique to estimate error terms, the random factor and overall error terms do not appear in our results

Source	df	F-ratio	Prob > F
Barnacles			
Year	1, 11.86	45.1683	**<0.0001***
WE	1, 10.71	26.7487	**0.0019***
Cue	1, 136.5	30.4552	**<0.0001***
WE × Cue	1, 136.5	0.2151	0.6435
Mussels			
Year	1, 8.837	10.1493	**0.0113***
WE	1, 10.15	0.1324	0.7234
Cue	1, 137.6	0.9823	0.3234
WE × Cue	1, 137	3.1575	0.0778

cues (crab = 2.93 ± 0.22 and control = 4.05 ± 0.22), and whelks in 2012 consumed fewer barnacles than whelks in 2013 (2.45 ± 0.20 and 4.53 ± 0.29, respectively). An ANOVA of the number of mussels eaten per *Nucella* showed no significant effects of Cue, WE, or their interactions (Table 4; Fig. 4b, inset values). However, *Nucella* did consume significantly more mussels in 2012 than in 2013 (0.37 ± 0.05 and 0.09 ± 0.07, respectively). In both years, *Nucella* consumed <50% of mussels available in each replicate, suggesting that mussels were never limiting. In 2012, *Nucella* consumed an average of 48.3% (0 to 95.9%) of available barnacles, suggesting that the latter were limiting in some replicates. However, in 2013, *Nucella* consumed <20% of barnacles available in each replicate. The similar barnacle consumption
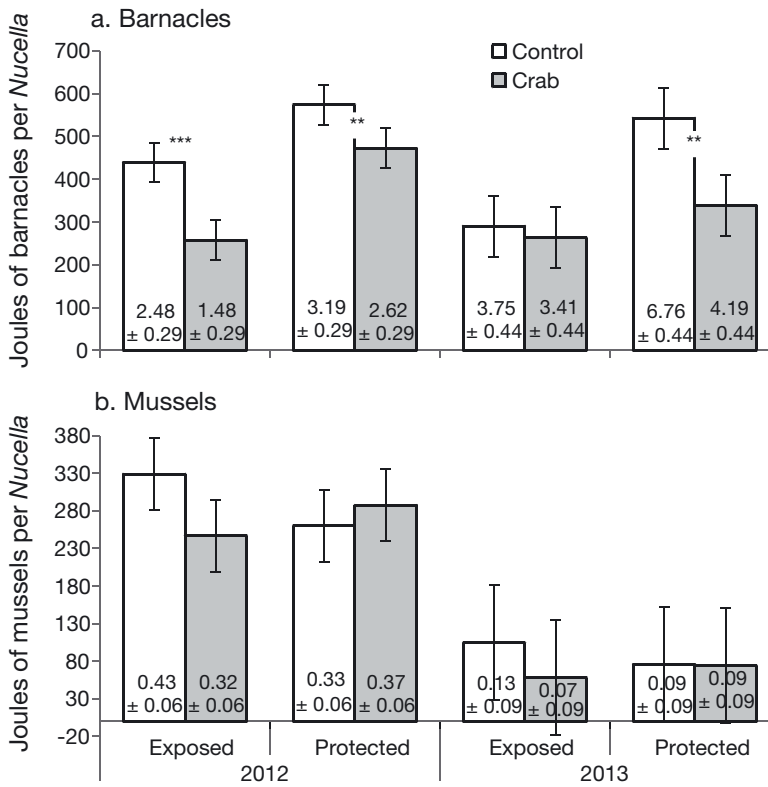
a. Barnacles

b. Mussels

Fig. 4. Prey foraging: Joules of (a) barnacles and (b) mussels consumed per *Nucella* (mean ± SE) in the prey foraging experiment. In a mesocosm, there were either waterborne cues of *Carcinus* (grey bars) or no crab control (white bars; see ANOVA results, Table 5). Numbers inside the bars represent the least-squares mean of the number of prey items consumed per *Nucella* ± SE. Asterisks indicate least-squares mean contrasts of Joules consumed in cue versus control treatments (*p ≤ 0.05, **p ≤ 0.01, ***p ≤ 0.0001)

Table 5. Prey foraging (ANOVA): Joules of barnacles and mussels consumed per *Nucella*. Cue treatment is either *Carcinus maenas* or control. Wave Exposure (WE) as in Table 2. Site was included as random factor nested within WE. Because JMP uses the restricted maximum likelihood technique to estimate error terms, the random factor and overall error terms do not appear in our results

Source	df	*F*-ratio	Prob > *F*
Barnacles			
Year	1, 10.67	2.0500	0.1808
WE	1, 132.9	11.2981	**0.0050***
Cue	1, 132.9	18.6404	**<0.0001***
WE × Cue	1, 132.9	0.6664	0.4158
WE × Year	1, 120	0.0234	0.8778
Cue × Year	1, 132.9	0.1882	0.6651
WE × Cue × Year	1, 132.9	4.6185	**0.0334***
Mussels			
Year	1, 8.818	9.4114	**0.0137***
WE	1, 10.12	0.1251	0.7308
Cue	1, 137.6	1.0036	0.3182
WE × Cue	1, 137.6	3.1754	0.08

DISCUSSION

In this study, we compared the behavioral responses of *Nucella lapillus* from wave-exposed and wave-protected sites. Across wave exposures, whelks appeared to recognize and respond to a common predatory crab, *Carcinus maenas*. When given the choice between 2 common prey items, *Semibalanus balanoides* and *Mytilus edulis*, *Nucella* consistently chose barnacles over mussels, suggesting optimal foraging decisions by choosing time-minimizing, energy-maximizing prey. Whelks from wave-protected sites consistently reduced foraging on barnacles in the presence of a predator, but whelks from exposed sites only reduced foraging on barnacles in the presence of a predator in 2012, not in 2013. Our results are consistent with previous work indicating that predator cues alter intermediate consumer foraging and result in strong positive effects on basal resources (Palmer 1990, Schmitz et al. 2004, Trussell et al. 2004, Freeman & Hamer 2009) and that the strength of trophic cascades is dependent on prey species consumed (Trussell et al. 2008); however, we add the realistic component of providing *Nucella* a choice between 2 abundant prey species. We confirm that trophic cascades are stronger on barnacles than mussels and conclude that predation cues likely have a similar effect on *Nucella's* prey choice, regardless of wave exposure at the site of origin and the availability of prey.

After being removed to laboratory conditions, *Nucella* will often continue to choose the same prey it consumed *in situ* (Dunkin & Hughes 1984, West 1986, Rovero et al. 1999, Sanford & Worth 2009). Accordingly, we had predicted that because *Nucella* from wave-exposed and wave-protected habitats are conditioned to different *in situ* mussel (and, to a lesser degree, barnacle) densities (Fig. 3), they would have different prey preferences and that these preferences might influence their responses to predators. Our results indicate that, regardless of predator cues, wave-exposed and wave-protected *Nucella* do not differ in their relative preference for barnacles over mussels. Mussels available *in situ* do not precondition *Nucella's* preferences (sensu Hughes & Dunkin 1984a,b). Interestingly, mussels were consumed in each treatment, indicating that a few *Nucella* from

each site (even wave-protected sites with no mussels) preferred mussels, suggesting individual dietary specialization (e.g. West 1986). However, when mussels are the sole basal food source, *Nucella* do transmit NCEs when they are taken from wave-protected sites (but not when taken from wave-exposed sites; Freeman & Hamer 2009). Although mussels may be a more energy-rich food source than barnacles, barnacles are more readily consumed and support higher shell growth rates than mussels (Burrows & Hughes 1990). Mussels have thick shells, require more handling time than barnacles, and have a lower ratio of energy gained per unit handling time (Dunkin & Hughes 1984, Hughes & Dunkin 1984a, Rovero et al. 1999). By consistently choosing barnacles (over mussels; Fig. 4), *Nucella* are not relying on prior experience with prey or ingestive conditioning and may be demonstrating optimum foraging (Sih 1980, Burrows & Hughes 1991a).

Site-to-site variation in available mussels and *Nucella's* prey choice in lab experiments also illustrate the lack of influence that prior conditioning has on subsequent foraging decisions. We expected that mussel-experienced whelks (i.e. those from Chamberlain; Fig. 2) would continue feeding on mussels in the lab if consumption is based on experience, but to the contrary, whelks from Chamberlain consumed mussels at similar rates to whelks from Kresge and Ocean Point (mussels consumed per *Nucella*: Chamberlain = 2.86 ± 0.25, Kresge = 2.67 ± 0.25, and Ocean Point = 3.28 ± 0.34). We found a negative correlation between the number of barnacles consumed per *Nucella* and the percent cover of barnacles at the site of origin (R^2 = 0.829, n = 6, p = 0.0116, barnacles per *Nucella* = 5.107 − 0.031 × percent cover barnacle; E. M. Dernbach unpubl. data). This pattern is more consistent with local *Nucella* populations consuming barnacles at a high rate and reducing barnacle cover *in situ*. Whelks collected from exposed sites consumed significantly fewer barnacles than whelks from protected sites, suggesting that a lasting effect of wave action suppresses *Nucella's* foraging rates (e.g. Freeman & Hamer 2009) without affecting the whelk's preference. Reduced foraging at wave-exposed sites may release barnacles at those sites from predator control and contribute to higher barnacle cover. Our results are more consistent with *Nucella* having a strong preference (sensu Murdoch 1969) for barnacles than a preference contingent on a prior diet that may include mussels (Dunkin & Hughes 1984, Hughes & Dunkin 1984a,b, West 1986, Burrows & Hughes 1991a,b, Hughes et al. 1992, Rovero et al. 1999).

Our experimental design incidentally showed that the impact of predator cues also was robust across wide density and size ranges of barnacles. Because of varying success with barnacle substrates, we used the natural set of barnacles on granite tiles in 2013 but existing intertidal cobbles in 2012. Consequently, the barnacles available to *Nucella* in 2013 were approximately 10 times more abundant, smaller (3.88 ± 0.097 vs. 5.11 ± 0.105 mm, respectively), and closer together than those in 2012. Whether due to optimal foraging (MacArthur & Pianka 1966) or strong preference that was not affected by the proportion of prey available (Murdoch 1969, West 1986), *Nucella's* energetic consumption was remarkably constant because whelks consumed more small barnacles in 2013 than in 2012 (Table 5, Fig. 4). Barnacle density in 2013 more closely approximated exposed-shore density, while density in 2012 approximated protected-shore barnacle density. In contrast, mussel density was consistent between years (n = 20 mussels per cage), yet mussel consumption was lower in 2013 than in 2012. We interpret mussel and barnacle consumption patterns as follows: *Nucella* consumed more barnacles, spent more time subduing and consuming (rather than searching for) barnacles, and therefore encountered and consumed fewer mussels in 2013 than in 2012.

Our experiments demonstrated that *Nucella* populations, from both protected and exposed shores, recognize and alter their behavior in response to *Carcinus* cues (Fig. 4) at both low and high prey densities (2012 and 2013 barnacle densities, respectively); however, exposed-shore whelks responded to *Carcinus* less consistently. A valid speculation would be that prior *in situ* exposure to predators influenced the whelks' responses. Whelks (e.g. *N. lamellosa*) that are preconditioned to crab cues are more likely to respond to subsequent cues (Edgell 2010). While there is anecdotal evidence that predators are more abundant at wave-protected sites (Menge 1978, Palmer 1990, Trussell 1996), when we surveyed mobile predators found in the shallow subtidal zone (< 5 m depth, 1 × 10 m transects, 5 to 25 at each site), we found no significant difference in either predator type or abundance between wave-exposed and wave-protected shores (Dernbach 2014). It is possible that at our sites, the differences in wave exposure were not substantial enough, sites were close enough, or predators were mobile enough to negate the wave-exposure effect. We surmise that, at least during the quiescent periods of our surveys, both wave-exposed and wave-protected *Nucella* experience predators and predator cues, and prior exposure does not explain a reduced response in wave-

exposed whelks. Fluid forces at wave-exposed sites may disrupt cue transmission (e.g. Smee & Weissburg 2006), moderating the wave-exposed whelks′ responses to subsequent predator cues. The tendency for reduced influence of crab cues on exposed-shore *Nucella* behavior (Fig. 4; Freeman & Hamer 2009) is likely due to a combination of the temporary disruption of cue transmission (Weissburg & Zimmer-Faust 1993, Smee & Weissburg 2006) and the displacement of mobile predators (Robles 1997).

Although foraging rates were reduced in both exposed and protected populations of *Nucella* in the presence of a predator, wave-exposed whelks ate significantly less across treatments than protected-shore whelks (Fig. 4). At each site, *Nucella* from exposed shores were significantly smaller than protected-shore whelks (p < 0.001; 15.17 ± 1.09 and 23.98 ± 1.09 mm, respectively; Dernbach 2014). Smaller whelks likely require less energy to maintain metabolic functions compared to larger individuals (Kleiber 1947, Gillooly et al. 2001, Nagy 2005). Differences in *Nucella* size between wave-protected and wave-exposed sites do not fully account for differences in foraging; when it was included as a covariate in foraging experiments, Shell Length was not significant (Dernbach 2014).

A growing number of studies emphasize the importance of NCEs, relative to CEs, and are predicated on an intermediate consumer′s perceived risk (Schmitz et al. 2004, Trussell et al. 2004, Hernández & Laundré 2005, Matassa & Trussell 2011). Because marine organisms rely heavily on waterborne cues, the primacy of NCEs in marine ecosystems must be considered in the context of factors that enhance or attenuate perception and reaction to cues (Weissburg et al. 2014). NCEs involving *Nucella* spp. are influenced by proximity to refuges (Matassa & Trussell 2011), prior exposure to predators (Edgell 2010), and wave exposure of the site of origin (Etter 1996, Freeman & Hamer 2009). Like many studies that provide elevated cue levels (Weissburg et al. 2014), our results are likely biased toward detecting NCEs. However, even with this bias, we did not find evidence for NCEs based on prey switching behavior in *Nucella* but do find support for the consideration of prior cue environment (wave exposure) as a factor influencing subsequent NCEs.

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