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Predation risk indirectly enhances survival of seaweed recruits but not intraspecific competition in an intermediate herbivore species

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Summary

1. Non-consumptive predator effects are an important driver in predator–prey interactions. While indirect effects of predation risk shape interspecific species interactions, e.g. in fuelling trophic cascades, knowledge about non-consumptive predator effects on intraspecific interactions among intimidated prey is scarce.

2. In laboratory experiments, we tested whether predation by male and female green crabs (*Carcinus maenas*) is stronger on small than on larger specimens of the periwinkle *Littorina littorea*, an important herbivore species in intertidal habitats of the temperate zone. Moreover, we asked whether size-specific differences in predation-induced mortality reflect as a stronger effect of predation risk (caused by nearby consuming crabs) on the foraging behaviour of more threatened periwinkles and ultimately on the recruitment success of the brown seaweed *Fucus serratus*. Furthermore, predator activity and prey abundance was measured in the field and the efficacy of predation risk on the survival of seaweed recruits was assessed in three field experiments with two different set-ups (open plots and crab exclosures).

3. Male crabs consumed smaller periwinkles more often than larger conspecifics, while females refused periwinkles as food. In summer, 80–90% of periwinkles in the field attained a size at which crab predation was minimal in laboratory assays. The observed up to 15-fold decrease in the consumption of seaweed recruits by periwinkles in the presence of nearby consuming crabs in laboratory assays was, however, independent of the size of periwinkles. Predation risk effects from the laboratory were only confirmed in field experiments using crab exclosures but not with open plots, suggesting an artefact due to trespassing by wild crabs in the open plot set-up.

4. *Synthesis*. Predation risk may not change intraspecific competition for food in *L. littorea*. Yet, risk effects on foraging behaviour of periwinkles that experience a low threat of real predation indicate that non-consumptive predator effects may affect prey population dynamics more strongly than consumptive predator effects. Thus predation risk effects may be indirectly beneficial for the survival of basal species like perennial seaweeds, as experimental evidence from field and laboratory experiments indicates.

Key-words: food web, *Fucus serratus,* meso-herbivores, periwinkles, phenotypic plasticity, plant–herbivore interactions, seaweed recruitment, trait-mediated, trophic interaction, water-borne info-chemicals

Introduction

Predicting patterns of species composition at the community and ecosystem level is the prime goal of ecology. Therefore, knowledge about the mode of how species interact is a fundamental prerequisite. Past research often investigated pair-wise

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species interactions, revealing the function of direct effects like competitive exclusion among species (e.g. Fine & Loya 2003). However, under natural conditions biological interactions occur among multiple species, permitting indirect effects. The latter can strongly inflate ecosystem complexity as indirect effects may dampen or even reverse the direct effects in the interaction between two species, often with strong effects on basal species like plants and seaweeds (reviewed e.g. in Wootton 2002; Hay *et al.* 2004; Ohgushi 2005; Creel & Christianson 2008).

Studies on density-mediated indirect effects, which fuel, for instance, trophic cascades (Lubchenco 1978; Simenstad, Estes & Kenyon 1978), have profoundly advanced our understanding of the role that consumptive effects have on the structure of communities and ecosystems. In addition, non-consumptive predator effects may result from the presence of risk cues, which are known to affect the behaviour, morphology and life history of prey (e.g. Ferrari, Wisenden & Chivers 2010). Schmitz *et al.* (2008) proposed generally opposing indirect predator effects on ecosystem properties and functions between non-consumptive and consumptive predator effects. This suggests that consideration of prey responses to predation risk may inflate our ability to explain contingencies in and the modulation of trophic interactions better than by addressing predation induced changes in prey density alone. In fact, classic examples of consumptive indirect effects in species interactions seem to result at least partially from the impact of intimidation on prey (Peckarsky *et al.* 2008; but see Kauffman, Brodie & Jules 2010). Non-consumptive predator effects should be more effective than consumptive effects because the latter attenuate through food chains, while the former remain strong (Preisser, Bolnick & Benard 2005), function immediately, and do both for the entire period that a predator is present (Werner & Peacor 2003).

Non-consumptive predator effects may be of particular importance in structuring marine ecosystems as the effects of intimidation, rather than those of consumption, are stronger in aquatic than in terrestrial ecosystems (Preisser, Bolnick & Benard 2005). The available evidence from marine systems suggests that non-consumptive predator effects can (i) shape patterns in prey distribution (Rochette & Dill 2000), (ii) enhance prey survival (Flynn & Smee 2010) and (iii) alter prey population dynamics and energy flow by changing mating success in prey (Koch, Lynch & Rochette 2007), reducing prey susceptibility to consumers (Yun *et al.* 2007), and/or changing feeding behaviour of intermediate consumers (Trussell, Ewanchuk & Bertness 2002). Less is known, however, about the influence of individual properties like sex, age or size of both predators and prey on strength and temporal variation of predation risk. Intraspecific variation in the ability to release or in the susceptibility to risk cues may increase the variability in the outcome of species interactions. Experimental evidence about sources for intraspecific variation in risk strength is scarce. According to Spooner, Coleman & Attrill (2007), the gastropods *Gibbula umbilicalis* and *Littorina littorea* showed no differences in their responses to risk cues originating from males and females of the predatory crab *Carcinus maenas*. In contrast, the level of satiation in juvenile prey (*Nucella lapillus*) determined their response to *C. maenas* risk cues (Vadas, Burrows & Hughes 1994). Prey size may be another source for intraspecific variation in the magnitude of risk effects. Optimal foraging theory predicts prey-size-dependent consumption rates of predators. Experimental evidence comes, for instance, from benthic ecosystems where *C. maenas* prefers blue mussels (*Mytilus edulis*) of intermediate size several-fold over smaller and larger conspecifics (Enderlein *et al.* 2003). Hence, size-specificity in predation-induced mortality may result in intraspecific variation of risk effects in prey, like herbivores, and thus concomitant shifts in the competition among conspecific prey individuals for resources, like seaweeds and plants, seem possible. Experimental evidence that predator traits can indirectly alter intraspecific and interspecific competition in prey is, to our knowledge, only available for freshwater food webs. There, the presence of nearby predators reduced the activity level and thus growth rate of small, but not of large, larvae of conspecific and heterospecific frog species (Peacor & Werner 2000). Furthermore, information on the seasonal variation in non-consumptive predator effects is scarce (but see Jacobsen & Stabell 1999), yet required for predicting the temporal scales at which, for instance, trait-mediated indirect interactions will be effective in seasonally-driven ecosystems, like those in the temperate zone.

This study addressed the effects of predation risk on changes in prey feeding behaviour in a temperate rocky intertidal food chain, using the predatory green crab *C. maenas* (L.), the herbivorous periwinkle *L. littorea* (L.), and recruits of the brown seaweed *Fucus serratus* (L.). Trussell, Ewanchuk & Bertness (2002) demonstrated that nearby consuming *C. maenas* had a strong, positive, indirect effect on the survival of seaweed recruits on a NW Atlantic rocky intertidal shore by changing periwinkle foraging behaviour. Patterns in trait-mediated interactions may, however, vary considerately across the Atlantic, like it has been demonstrated for phenotypic plastic responses in seaweed–grazer interactions (Long & Trussell 2007). This simple food chain also exists on NE Atlantic shores, where *L. littorea* may reach densities of > 400 individuals m^{-2} (Eschweiler, Molis & Buschbaum 2009), a level at which intraspecific competition may occur in *L. littorea* (Petraitis 2002). Yet, knowledge on trait-mediated indirect interactions in this food chain is missing for the NE Atlantic and their potential in affecting intraspecific competition in periwinkles has not been studied altogether. In laboratory experiments, we tested with NE Atlantic organisms at two times (i) whether the consumption of *L. littorea* by *C. maenas* was size-dependent; (ii) whether *L. littorea* consumed less *F. serratus* recruits in the presence than in the absence of consuming *C. maenas*, and (iii) whether changes in *L. littorea* foraging behaviour to predation risk were dependent on the size of *L. littorea*. Furthermore, we assessed in manipulative experiments whether findings from laboratory assays hold under field conditions.

Materials & methods

STUDY SITE

Field experiments were conducted and the organisms used in laboratory experiments were collected in the mid-intertidal at Nordwatt Helgoland, Germany (54°11′ N, 7°11′ E), NE Atlantic. Nordwatt is a moderately wave-exposed intertidal platform with semi-diurnal tides of an average range of 2.5 m. The emergent substratum consists of red sandstone, scarcely scattered flint boulders (max. Ø 25 cm) and small patches of shell. A previously reported mussel bed (Janke 1986) at the study site had disappeared. Presently, few mussels exist there, with specimens < 40 mm hiding in crevices and those > 40 mm attaching to rock surfaces (M. Molis, pers. obs.). The latter attain a size of reduced vulnerability to *C. maenas* predation (Enderlein *et al.* 2003). The mid-intertidal is characterized by two persistent stages of a *Fucus*-habitat (Bartsch & Tittley 2004). One area is dominated by a dense canopy of *F. serratus*, while the other area, where the field experiment was conducted, is 30% covered by *F. serratus*, *F. vesiculosus and F. spiralis* (hereafter Littorina Barren). *Fucus*-associated understorey algae and invertebrates exist in both areas with the periwinkle *L. littorea* as the dominant herbivore occurring year-round at the study site (see Bartsch & Tittley 2004; Reichert *et al.* 2008 for details on species composition). In contrast, *C. maenas* is absent from Nordwatt between late October and March (M. Molis, pers. obs.), when it is located in the relatively warmer subtidal habitats until water temperature reaches 6–8 °C again in spring (D. Klings, pers. comm.).

EXPERIMENTAL DESIGN AND SET-UP

Activity of C. maenas and abundance of L. littorea

To characterize activity patterns of *C. maenas* and the population structure of *L. littorea*, the abundance of both was recorded at Littorina Barren. To estimate the activity of *C. maenas*, one non-baited trap was set up during low tide at 6 days between 13 June and 11 September 2008, and at 30 days between 10 June and 28 July 2009. After 24 h of deployment, number and sex of trapped *C. maenas* were recorded and their carapace width measured to the nearest 0.01 mm with digital callipers. The density of *L. littorea* was first estimated in September 2007 and hereafter about every 3 months until September 2008. At each sampling date, all *L. littorea* specimens were collected from 12 randomly chosen 1 m^2 large non-permanent plots and transported to the laboratory of the Biologische Anstalt Helgoland. Here, the size of each specimen was measured with digital callipers to the nearest 0.01 mm as the maximum distance of the shell parallel to the plane of the aperture. The abundance of *C. maenas* of different sex was compared with a paired *t*-test from 36 daily measurements. Using a two-way repeated-measure ANOVA, the density of *L. littorea* of different size classes encountered per square metre (within-subject factor, fixed, four levels) was compared among seasons (grouping factor, random, five levels).

Consumption rates of C. maenas

To assess whether *C. maenas* prefers *L. littorea* of a certain size and whether this preference was sex-dependent, one multi-choice feeding assay was conducted in the laboratory from 6 to 20 September 2007 (late summer) and two multi-choice assays between 18 June and 22 July 2008 (early summer). Two days before the start of the experiment in 2007, single male *C. maenas* (mean ± SD carapace width 68.13 ± 5.07 mm) were introduced to feeding arenas without food. As feeding arenas we used transparent plastic aquaria (19 × 17.5 × 32.5 cm), filled, on average, with 8.1 L of seawater. Each aquarium (= experimental unit, EU) was individually supplied with a uni-directional flow of ambient filtered (sand and cotton) and aerated seawater (16.5 ° and 18 °C in early and late summer, respectively) at a rate of *c.* 4 L h^{-1}. Seawater was directly pumped from the nearby (< 50 m) North Sea into the laboratory at the Biologische Anstalt Helgoland. At the beginning of the 2007 experiment, 20 feeding arenas were populated with four *L. littorea* from each of the four size classes (i) < 18 mm, (ii) 18 to < 20 mm, (iii) 20 to < 23 mm, and (iv) ≥23 mm (total of 16 periwinkles per EU). In 2008, the experiment was repeated with male *C. maenas* (68.67 ± 3.88 mm) and extended by 20 additional feeding arenas, to which *L. littorea* were added as in the 2007 experiment, but which contained one female *C. maenas* (55.89 ± 8.27 mm) each. The number of consumed *L. littorea* per size category was recorded daily during the 14-day-long feeding assays. From each EU where *C. maenas* was feeding, the total number of *L. littorea* of different size classes that where consumed during assays were used as response variables. Using a repeated-measures ANOVA, *C. maenas* consumption rates among the four size categories of *L. littorea* (within-subject treatments, fixed, four levels) were compared between early and late summer (random, two levels).

Feeding preference of C. maenas

To test whether *C. maenas* shows a preference between different types of mollusc prey, multi-choice feeding assays were conducted in the laboratory. On 6 September 2007, 20 aquaria were set up (specifications of the general set-up as above), containing each one blue mussel (*M. edulis* (L.)), one oyster (*Crassostrea gigas* Thunberg 1793), two *L. Littorea* (one specimen 18 to < 20 mm and the other 20 to < 23 mm), and one male *C. maenas*, starved for 2 days prior to assays. The identity and number of consumed prey items was recorded at the end of the 7-day-long experiment and used as the response variable that was analysed by resampling without replacement, using a Monte Carlo analysis with 10 000 permutations (Bärlocher 1999).

Non-consumptive indirect predator effects

Two laboratory and three field experiments were conducted, to assess the non-consumptive effects of *C. maenas* on *L. littorea* consumption rates. *Littorina littorea* food consisted of 6- to 8-week-old *F. serratus* recruits. To generate recruits, eggs were fertilized in the laboratory and zygotes seeded onto unglazed ceramic tiles (9.6 × 9.6 cm). After 6 to 8 weeks of incubation at 15 °C and 54 μmol photons s^{-1} m^{-2} in a 12:12 dark:light rhythm, zygotes developed into *c.* 2-mm-tall recruits.

At the beginning of the laboratory experiments, two ceramic tiles covered with *F. serratus* recruits were placed in each aquarium (specifications see above). Each aquarium was divided by a green plastic mesh (1 mm mesh size) into an up- and downstream compartment of equal size. In the upstream compartment, *C. maenas* could hide in an 8-cm-long PVC pipe (Ø 9 cm). The downstream compartment was further divided by an opaque PVC plate into two chambers of equal size, with each chamber containing one ceramic tile covered with *F. serratus* recruits (Fig. 1). Experiments were conducted in early and late summer from 19 to 27 June 2008 and 14 to 22 September 2008, respectively. Treatments included (i) controls, containing in both downstream chambers only tiles covered with *F. serratus* recruits (Fig. 1); (ii) *L. littorea* grazing aquaria, in which three small

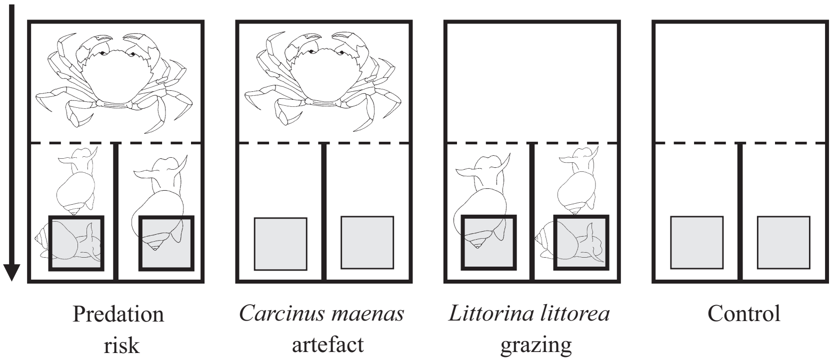

Fig. 1. Experimental set-up of laboratory experiments testing for non-consumptive predator effects. Arrow indicates direction of water flow. Stippled lines indicate mesh, dividing aquaria into up- and downstream compartments. Thick solid lines indicate opaque PVC plates separating downstream compartments into two chambers containing either small (< 18 mm) or large (≥ 20 mm) *Littorina littorea* feeding on *Fucus serratus* recruits grown on ceramic tiles (grey quadrates). Thick-lined quadrates indicate tiles used for testing the effects of predation risk on intraspecific competition in *L. littorea*.

(< 18 mm) and two larger (≥ 20 mm) periwinkles were each randomly allocated to one downstream chamber in addition to tiles covered with *F. serratus* recruits; (iii) predation risk aquaria, which were set up like *L. littorea* grazing aquaria but contained in addition a single male *C. maenas* (47.9 ± 8.6 mm) in the upstream compartment and (iv) *C. maenas* artefact aquaria, in which upstream compartments contained a single male *C. maenas* (48.6 ± 7.3 mm), while each downstream compartment contained one tile covered with *F. serratus* recruits but no *L. littorea*. Assuming that the soft body mass of periwinkles is a good proxy for grazing impact, *L. littorea* soft body mass was non-destructively calculated prior to experiments to ensure comparable *L. littorea* grazing impact in chambers containing small and large periwinkles. Adopting the methods described in Trussell (2000), we determined the soft body mass of 64 *L. littorea* between 12 and 28 cm shell length (four specimens per 1 mm interval) for converting shell length into soft body mass (linear regression: $y = 0.2863x$, $n = 64$, $r^2 = 0.831$). The soft body mass of small and large *L. littorea* in both chambers of each aquarium was a non-significant ≤ 1% different (Student's *t*-test: early summer: $t_{14} = 0.63$, $P = 0.536$; late summer: $t_{38} = 0.02$, $P = 0.988$). Consequently, we assumed identical overall consumption impact in chambers containing small or large *L. littorea*.

Seven shell-crushed *L. littorea* (< 18 mm) were added as *C. maenas* food to upstream compartments. Experiments in early and late summer comprised a total of 16 and 40 aquaria, respectively, which were grouped in quartets on separate tiers, and irradiated with light tubes at 34 μmol photons s^{-1} m^{-2}. Each of the four treatments was present per quartet and was randomly positioned on each tier, resulting in a sample size of four and ten in the early and late summer experiment, respectively. Assays were terminated when *F. serratus* recruits of at least five tiles were grazed down to ≤ 10%. Differences in the consumption of *F. serratus* recruits by *L. littorea* of different size (within-subject factor, fixed, two levels) in the presence and absence of predation risk (grouping factor, fixed, two levels) were analysed with repeated-measures ANOVA. Separate two-way ANOVAS compared grazing impact of large and small *L. littorea*, respectively, with controls to assess main and interactive effects of predation risk and *L. littorea* grazing on survival of *F. serratus* recruits.

Three field experiments were conducted to assess whether the presence of nearby consuming *C. maenas* affected the grazing behaviour of *L. littorea*. Two field experiments were conducted from 16 to 24 July and 9 to 17 September 2008, in which the set-up from Trussell, Ewanchuk & Bertness (2002) was adopted. In both experiments, ten circular (Ø 1.2 m) plots were randomly positioned at a minimum distance of 6.5 m at Littorina Barren. Each plot consisted of nine perforated orange PVC pipes (Ø = 20 cm, 15 cm high) that were bolted evenly spaced in a circular pattern to the substratum at the perimeter of each plot. The open ends of each pipe (= crab cage) were closed with a green plastic mesh of 0.1 cm mesh size. In the centre of each plot, four cubical cages (= *Littorina* cages) made of green plastic mesh (mesh size 4 mm) were bolted to the substratum. On the day the experiments started ceramic tiles (9.6 × 9.6 cm) with *F. serratus* recruits were fixed inside each *Littorina* cage. Furthermore, two (early summer) or five (late summer) *L. littorea* (< 18 mm) were randomly added to two of the four *Littorina* cages of each plot (= grazing treatment), while no *L. littorea* were added to the remaining two *Littorina* cages of each plot (= control). The number of *L. littorina* was increased in late summer to ensure that missing effects in early summer were not caused by low grazing pressure. Finally, one male *C. maenas* (carapace width > 58 mm) together with seven shell-crushed *L. littorea* (< 18 mm) for food were added to each crab cage of five randomly chosen plots (predation risk treatment), while seven shell-crushed *L. littorea* without *C. maenas* were added to crab cages of the remaining five plots (control). Five of the 90 *C. maenas* imprisoned in both experiments died (5.5%) but casualties never exceeded more than one individual per plot. Dead *C. maenas* were not replaced. The third field experiment used a different set-up and was conducted from 16 to 26 July 2009. Instead of using nine small crab cages in each plot, circular (Ø 1.7 m) plastic cages (4 mm mesh size) were bolted to the shore at Littorina Barren. Each of these 10 cages (= crab arena) was 30 cm high and closed at the bottom and top with the same plastic mesh. In the centre of each crab arena, four *Littorina* cages (specifications see above) were fixed with cable ties to the bottom mesh. Ten *C. maenas* were added to half of the crab arenas and were fed daily with 10 shell-crushed *M. edulis*. In addition, *L. littorea* were added at ambient density to crab arenas. Field experiments testing for the effects of predation risk (two levels, fixed) on periwinkle grazing (two levels, fixed) were analysed by three-way nested ANOVAS, with plots nested within predation risk.

Assessment of *L. littorina* consumption

A 1-cm band along the margin of tiles was excluded from sampling to avoid edge effects. To determine the density of *F. serratus* recruits, all recruits from 21 randomly selected 1-cm^2 sub-samples (= 36% of the tile area that was sampled) were counted on each tile prior to and at the end of experiments, using a stereo microscope (12× magnification). The proportion of the number of remaining recruits was calculated and used as the response variable in the statistical analyses.

STATISTICAL ANALYSIS

Prior to the analyses, proportional data were arcsin-transformed, normality of differences confirmed with Kolmogorov–Smirnov test (paired *t*-test), and homogeneous variances confirmed with Cochran's test. Data showing heterogeneous variances were log-transformed to meet the assumptions. In case heterogeneous variances persisted after transformation, the level of significance was reduced to $\alpha = 0.01$. The assumption of sphericity was tested for dependent data with Mauchly's test if more than two within-subject treatments occurred (Quinn & Keough 2002). When the sphericity assumption was violated, *F*-tests were adjusted using the Greenhouse–Geisser estimate and adjusted degrees of freedom were reported. *Post hoc* comparisons were done with Tukey's Honestly Significant Differences test.

Results

CARCINUS MAENAS ACTIVITY AND ABUNDANCE OF *L. LITTOREA*

A total of 449 *C. maenas* with an average (± SD) carapace width of 48.3 (± 11.31) (males) and 40.6 (± 6.92) mm (females), were encountered at Littorina Barren. There were significantly 4.5 times more male than female *C. maenas* present at the study site (paired *t*-test: $t_{35} = 9.51, P = 0.000$).

Up to 829 *L. littorea* specimens per square metre were collected at the study site. The total number of *L. littorea* per square metre was not significantly different between sampling events (two-way RM-ANOVA: $F_{4;55} = 2.28, P = 0.072$, Fig. 2). Yet, there were significant differences in the abundance of *L. littorea* among size classes (two-way RM-ANOVA: $F_{1.4;165} = 68.68, P < 0.0001$, Fig. 2). The smallest *L. littorea* were, on average, 49%, 72% and 38% less abundant than conspecifics of 17–20 mm, 20–23 mm and > 23 mm in shell height, respectively. Moreover, *L. littorea* of 20–23 mm in height were, on average, 1.8 and 2.2 times more abundant than conspecifics of 17–20 mm and > 23 mm, respectively, with a similar mean density of *L. littorea* between the latter two size classes (Fig. 2). Differences in the density of differently sized *L. littorea* were dependent on the time of sampling (two-way RM-ANOVA: $F_{5.6;165} = 12.75, P < 0.0001$). While *L. littorea* population structure followed a similar trend among seasons, magnitude of relative differences in abundance of periwinkles of different size classes varied seasonally. For instance, in both early (July) and late summer (September) of 2008, the density of the smallest *L. littorea* was, on average, eight and four times lower than the density of 20–23 mm and > 23 mm large conspecifics, respectively, while a similar density of *L. littorea* of some sizes was recorded in April 2008 (Fig. 2).

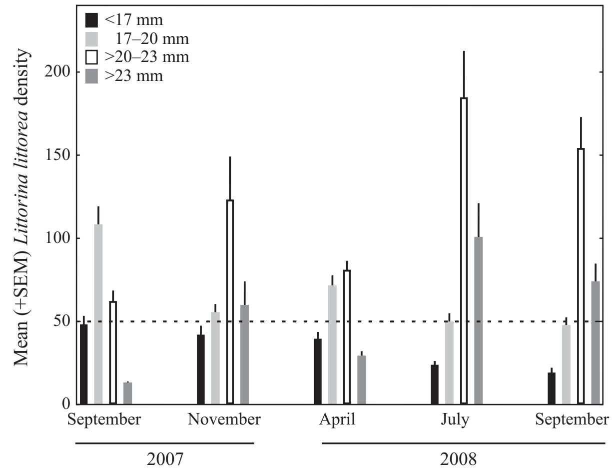

Fig. 2. Mean (+SEM) number of individual *Littorina littorea* per square metre of four different size classes at Littorina Barren between September 2007 and 2008. Stippled line = average density of *L. littorea* at NW Atlantic site of the Trussell, Ewanchuk & Bertness (2002) study. $n = 12$.

CONSUMPTION RATES BY *C. MAENAS*

None of the female *C. maenas* consumed *L. littorea*, while 50% and 45% of the male *C. maenas* consumed *L. littorea* in early and late summer, respectively. Female *C. maenas* were a significant 18% smaller than males (Student's *t*-test: $t_{18} = 5.65, P < 0.001$), whereas consuming males were a non-significant 4% larger than non-consuming males (Student's *t*-test: $t_{16} = 1.13, P = 0.243$). Male *C. maenas* significantly preferred small (< 18 mm) to larger *L. littorea*, at a rate that was, on average, five times higher (two-way RM-ANOVA: $F_{3,48} = 20.32, P < 0.0001$, Fig. 3). This preference persisted during the study period, as indicated by a missing interaction between *L. littorea* size and season (two-way RM-ANOVA: $F_{3,48} = 1.37, P = 0.263$). Furthermore, feeding preferences of *C. maenas* were not different between seasons (two-way RM-ANOVA: $F_{1,16} = 0.03, P = 0.878$). With the exception of one assay, the two smallest *L. littorea* per EU were consumed prior to the larger conspecifics.

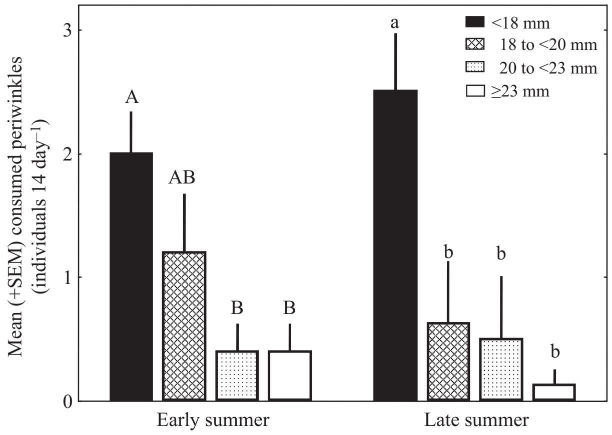

Fig. 3. Mean (+SEM) number of consumed *Littorina littorea* of different size categories by *Carcinus maenas* during 14-day-long feeding assays. Consumption rates on size categories sharing a letter were not significantly different. $n = 9$ and 10 in early and late summer, respectively.

FEEDING PREFERENCE OF *C. MAENAS*

Carcinus maenas preferred *C. gigas* and *M. edulis* significantly to *L. littorea* (resampling: $P < 0.0001$). Ten *C. maenas* consumed both *C. gigas* and *M. edulis*, while five *C. maenas* consumed either *M. edulis* or *C. gigas*. None of the *L. littorea* were consumed.

NON-CONSUMPTIVE PREDATOR EFFECTS (LABORATORY)

In early summer, the presence of nearby consuming *C. maenas* was significantly beneficial for the density of *L. littorea*-exposed *F. serratus* recruits (two-way RM-ANOVA: $F_{1,6} = 179.88$, $P < 0.001$). Fifteen times more recruits remained on tiles in the presence of *L. littorea* in aquaria with than without *C. maenas* (Fig. 4a). The density of *F. serratus* recruits was neither significantly different between treatments using small and large *L. littorea* ($F_{1,6} = 1.14$, $P = 0.328$), nor was the effect of predation risk dependent on the size of *L. littorea* (Size × Predation Risk interaction: $F_{1,6} = 2.86$, $P = 0.142$). Using 2 two-way ANOVAS, recruit survivorship of tiles exposed to both, small or large *L. littorea*, was dependent on the presence of *C. maenas* (Table 1). Regardless of the size of *L. littorea*, *F. serratus* recruit density was not significantly different between aquaria with and without *L. littorea* when *C. maenas* was present. However, when *C. maenas* was absent, significantly fewer recruits (i.e. 15 times) remained on tiles with small as well as with large *L. littorea* than on tiles without *L. littorea* (Fig. 4a).

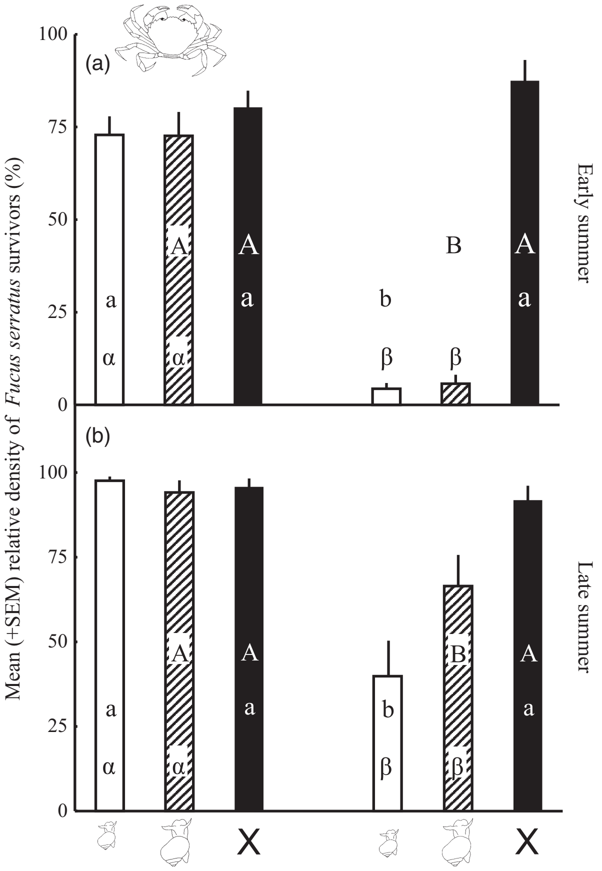

Fig. 4. Laboratory assays. Mean (+SEM) percent of *Fucus serratus* recruits remaining on settlement tiles after 8-day-exposure to small (white bars), large (cross-hatched bars) or without (black bars) *Littorina littorea* in the presence and absence of non-lethal *Carcinus maenas* in (a) early and (b) late summer 2008. Treatments sharing a letter were not significantly different. Greek letters illustrate statistical results from RM-ANOVAS between small and large *L. littorea*, while minor and capital letters illustrate results from two-way ANOVAS comparing grazing effects of small and large *L. littorea*, respectively, with *L. littorea*-free control treatments (see Materials and methods for details). $n = 4$ and 10 in early and late summer, respectively. X marks *L. littorea*-free control treatments, crab denotes treatments with predation risk.

In late summer, *L. littorea* grazing was significantly affected by the presence of nearby consuming *C. maenas* (two-way RM-ANOVA: $F_{1,18} = 40.54$, $P < 0.001$). The density of *F. serratus* recruits in the presence of *L. littorea* was, on average, 1.8 times higher in aquaria with than without *C. maenas* (Fig. 4b). Recruit density was not significantly different between treatments using small and large *L. littorea* (two-way RM-ANOVA: $F_{1,18} = 2.29$, $P = 0.148$). Furthermore, a non-significant interaction between predation risk and *L. littorea* size indicates that the presence of nearby consuming *C. maenas* had a similar effect on the grazing impact of large and small *L. littorea* (two-way RM-ANOVA: $F_{1,18} = 3.81$, $P = 0.067$). Two 2-way ANOVAS revealed that survival of *F. serratus* recruits exposed to either small or large *L. littorea* was a significant 2.3 and 1.4 times, respectively, lower on tiles with than without *L. littorea*, but only in aquaria where *C. maenas* was absent from the upstream compartment as indicated by the significant *Littorina* × Risk cue interaction (Table 1, Fig. 4b).

NON-CONSUMPTIVE PREDATOR EFFECTS (FIELD)

Littorina littorea grazing significantly reduced the density of *F. serratus* recruits in early and late summer 2008 and summer 2009 by, on average, 26%, 45% and 50%, respectively (Fig. 5). This effect was not changed by the presence of nearby consuming *C. maenas* in early and late summer 2008 (Table 2). Using the different experimental set-up in 2009; however, the effect of *L. littorea* grazing on recruit density of *F. serratus* was dependent on the presence of *C. maenas* as indicated by a significant *L. littorea* × *C. maenas* interaction (Table 2). In the absence of *C. maenas*, *L. littorea* reduced the recruit density of *F. serratus* by a significant 65%, whereas the grazing impact of *L. littorea* was significantly weaker (about 33% reduction in recruit density), albeit significant, in the presence of nearby consuming *C. maenas* (Fig. 5).

Discussion

Carcinus maenas preferred small over larger *L. littorea* in early and in late summer. Furthermore, the presence of nearby consuming *C. maenas* altered at both times the foraging behaviour of *L. littorea* under laboratory conditions, but did so in the field only when large crab exclosures were used. Despite the observed size-dependent risk of consumption by *C. maenas*,

Table 1. Results of two-way ANOVAs. Comparing the effects of grazing by (A) small and (B) large periwinkles (*Littorina littorea*) to grazer-free controls on the density of *Fucus serratus* recruits in early ($n = 4$) and late ($n = 10$) summer in the presence and absence of risk cues of predatory crabs (*Carcinus maenas*) during 8-day-long laboratory assays. d.f., degrees of freedom; MS, mean square; significant results in bold

	Early summer				Late summer			
Source	d.f.	MS	*F*	*P*	d.f.	MS	*F*	*P*
A								
Small *Littorina* (L)	1	3835	51.01	**< 0.001**	1	2506	9.57	**< 0.001**
Risk cue (R)	1	1732	23.03	**< 0.001**	1	5846	22.31	**< 0.001**
L × R	1	2967	39.46	**< 0.001**	1	5729	21.86	**< 0.001**
Residual	12	75			36	262		
B								
Large *Littorina* (L)	1	4132	108.7	**< 0.001**	1	476	1.69	0.202
Risk cue (R)	1	1764	46.38	**< 0.001**	1	1600	5.67	**0.023**
L × R	1	3009	79.11	**< 0.001**	1	**1539**	**5.45**	**0.025**
Residual	12	38			36	282		

the level of intimidation was similar in small and large *L. littorea* in laboratory experiments.

Several findings of this study intuitively suggest that consumptive effects of *C. maenas* on the *L. littorea* population and thus beneficial indirect effects on recruit survival of *F. serratus* should be of limited impact. First, the consumption of periwinkles by *C. maenas* was dependent on the size of snails. Small periwinkles (< 18 mm) were more often consumed by green crabs than larger conspecifics. This size-specific preference was apparent in laboratory experiments conducted in early and in late summer. As 80–95% of the periwinkles encountered at the study site were larger than the preferred size class, the majority of the adult *L. littorea* population dwell under a relatively low *C. maenas* predation pressure. Studies by Buschbaum *et al.* (2007) and Perez *et al.* (2009) corroborate patterns in size-specific consumption of *L. littorina* by green crabs on NE and NW Atlantic shores. Like other molluscs, larger periwinkles may lower or even escape predation by shell-thickening (e.g. Freeman & Byers 2006). Hereby, infestation by shell-boring organisms like the polychaete *Polydora ciliata* can modify shell strength in *L. littorea*, reducing the size refuge from crab predation for periwinkles (Buschbaum *et al.* 2007). Yet, the Helgoland population of *L. littorea* appeared hardly infested by *P. ciliata* or trematodes (Eschweiler, Molis & Buschbaum 2009), indicating that larger *L. littorea* should be relatively safe from green crab predation at our study site. Second, only males of the *C. maenas* population on Helgoland consumed *L. littorea*. This can be due to sexual dimorphism in claw morphology and possibly the observed smaller size of females to males, favouring the latter in crushing mollusc prey (Elner 1980). According to trap samples, at least 22% of *C. maenas* individuals were females so that *L. littorina* will be consumed by a maximum of 78% of the individuals that constitute the *C. maenas* population at the study site. Third, only half of the male *C. maenas* consumed periwinkles during 14-day-long assays. A similar size of consuming and non-consuming *C. maenas* suggests that other factors than morphological features could explain this pattern. This finding, in combination with the observed strong rejection of periwinkles by *C. maenas* when alternative food is present, suggests that *L. littorea* is an unattractive diet for *C. maenas*. Nevertheless, occasional presence of cracked *L. littorea* shells at the study site (M. Molis, pers. obs.) indicates that some periwinkle consumption by shell-crushing predators like *C. maenas* takes place.

In the light of this relatively low predation pressure by *C. maenas* on *L. littorea*, the strong reduction in food intake by periwinkles in the presence of nearby consuming *C. maenas* in laboratory assays is striking. Besides a 15-fold higher chance for *F. serratus* recruits to survive *L. littorea* grazing in the presence than in the absence of *C. maenas*, it is even more noticeable that the number of survivors was almost identical between treatments with and without *L. littorea* when crabs were present. This indicates that nearby consuming *C. maenas* induced such a high level of intimidation that grazing by *L. littorea* was almost completely 'switched off'. This strong positive indirect effect of predation risk on *F. serratus* recruit survival corroborates results of the field study by Trussell, Ewanchuk & Bertness (2002). Thus, non-consumptive predator effects can be beneficial for the survival of basal species (e.g. Coleman *et al.* 2007), affect energy transfer (Trussell, Ewanchuk & Matassa 2006a) and probably ultimately species composition and functioning of communities (Schmitz *et al.* 2008). However, our study also indicates that the strength of risk effects can vary temporally. Intimidation of periwinkles was at its maximum when *F. serratus* ceased reproduction (July–August) and at its minimum during the main reproductive period of *F. serratus*, i.e. from September to May (Kornmann & Sahling 1993), which is also the period when *C. maenas* overwinters offshore. A strong predation risk effect in early summer should maximize survival of small recruits that settled during spring, while the higher recruitment of *F. serratus*, taking place at a time when the indirect protection by *C. maenas* from periwinkle grazing will be less strong, i.e. in late summer, may compensate grazing-induced recruitment losses.

Our study revealed that survivorship of *F. serratus* recruits was similar between small and larger periwinkles in the presence of nearby consuming *C. maenas*. In contrast to the findings by Vadas, Burrows & Hughes (1994) using dogwhelks (*N. lapillus*), our finding indicates that for *L. littorea* the level of intimidation was independent of body size. Therefore,

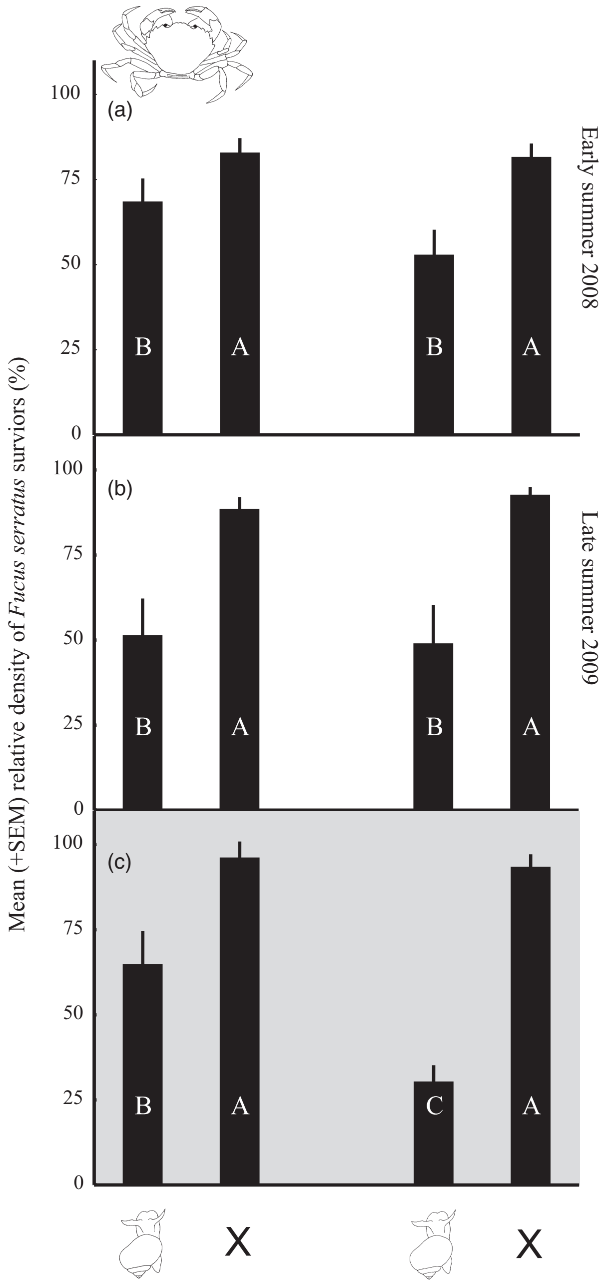

Fig. 5. Field assays. Mean (+SEM) percentage of *Fucus serratus* recruits remaining on settlement tiles after 8 (a, b) or 10 days (c) with or without *Littorina littorea* in the presence and absence of nearby consuming *Carcinus maenas*. Treatments sharing a letter were not significantly different. $n = 5$, grey background marking = experiment using crab arenas, crab denotes treatments with predation risk.

non-consumptive predator effects seem to have no effect on intraspecific competition for food in *L. littorea*. According to the high predation rate of small periwinkles by *C. maenas*, we expected small *L. littorea* to be significantly more intimidated by predation risk than larger specimens and, thus, survival of *F. serratus* recruits in the presence of nearby consuming *C. maenas* to be significantly lower when exposed to larger than to small periwinkles. Nevertheless, the lack of such patterns provides evidence of the importance of non-consumptive relative to consumptive predator effects in this simple food chain. Due to consumptive predator effects, an enhancement of the recruitment success of *F. serratus* is limited to the reduction of the grazing impact by small periwinkles (< 18 mm), which crabs preferably remove from the population. In contrast, predation risk reduced the grazing impact of small and larger periwinkles regardless of real predation threat equally strong, suggesting that non-consumptive predator effects will lower the grazing impact of all periwinkles. Therefore, recruitment success of *F. serratus* should be much higher due to non-consumptive rather than consumptive predator effects. Thus, periwinkle food, like seaweeds, should benefit more from the intimidation than the consumption of *L. littorea* by *C. maenas*. Although we did not directly test this, this statement is corroborated by experimental evidence from other studies on the contribution of risk effects to the net effect of predation. These studies suggest that non-consumptive predator effects can be at least as strong as the consumptive effects of a predator (Peacor & Werner 2001; Trussell, Ewanchuk & Matassa 2006b). Moreover, our study shows that even relatively unattractive prey responds strongly to predation risk, suggesting that non-consumptive predator effects may affect a relatively broad range of species and not only preferred prey, while consumptive predator effects should affect attractive prey disproportionately stronger. This indicates that non-consumptive predator effects may increase the connectivity among species more than consumptive effects do, with possible positive effects on ecosystem function (Schmitz *et al.* 2008) and diversity (Schmitz 2006).

Only our field experiments using large crab exclosures (2009 experiment) corroborate beneficial effects of predation risk on survival of *F. serratus* recruits observed in laboratory assays. This effect was mainly caused by a stronger reduction in recruit density from grazing *L. littorea* in the absence of *C. maenas* when crab exclosures instead of open plots (used in 2008 experiments) were used. Perhaps, open plots were trespassed by wild *C. maenas* thereby intimidating *L. littorina* in control plots equally strong to conspecifics inside risk plots. Differences between Trussell, Ewanchuk & Bertness (2002) and our 2008 experiments in *L. littorea* grazing impact in the absence of risk cues may be due to a lower activity level of *C. maenas* at the former than at our study site. Trussell, Ewanchuk & Bertness (2002) did not report on the activity or abundance of *C. maenas* at their study site. Our data from trap samples suggest that twelve *C. maenas* trespass on average daily through a plot. Although it is unknown whether this exposure level will sufficiently affect periwinkle foraging behaviour, models by Lima & Bednekoff (1999) suggest that irregular exposure to predator cues could elicit a stronger anti-predator behaviour than a constant level of exposure.

In contrast to our laboratory experiments and the field study by Trussell, Ewanchuk & Bertness (2002), recruit density was in all three field experiments more strongly reduced by *L. littorea* grazing in the presence of *C. maenas* than in risk plots where *L. littorea* was absent. This suggests that non-consumptive effects among *C. maenas*, *L. littorea* and *F. serratus* are not general and that perhaps some

Table 2. Field experiments. Results of nested three-way ANOVAS comparing the effects of *Littorina littorea* grazing on the number of *Fucus serratus*-recruits in the presence and absence of risk cues of the predator *Carcinus maenas*. Elimination of error term L × Plot(Risk cue) and recalculation of residuals was done for the 2009 experiment only, after verifying that σ^2 L × Plot(Risk cue) = 0, i.e. not significant at $\alpha = 0.25$, with used denominator mean square (MQ_{den}) for each source of variation shown in column MQ_{den}. *Pooled* term = L × Plot(Risk cue) + Residual, $d.f._{pooled}$, degrees of freedom after elimination of error term L × Plot(Risk cue), significant results at $\alpha = 0.05$ in bold, $n = 5$

	Early summer 2008				Late summer 2008			Early summer 2009				
Source	d.f.	MQ	*F*	*P*	MQ	*F*	*P*	$d.f._{pooled}$	MQ	*F*	*P*	MQ_{den}
Risk cue (R)	1	543.7	3.16	0.091	26.58	0.087	0.772	1	2103	10.61	**0.012**	Plot(Risk cue)
Littorina (L)	1	2408	14.01	**0.001**	8474	27.62	**< 0.001**	1	5549	50.13	**< 0.001**	pooled
R × L	1	214.0	1.25	0.278	32.42	0.11	0.749	1	1415	12.79	**0.001**	pooled
Plot(Risk Cue)	8	292.4	1.70	0.160	513.9	1.68	0.166	8	198	1.79	0.122	pooled
L × Plot(Risk cue)	8	258.0	1.50	0.219	571.5	1.86	0.124		105	0.93	0.517	Residual
Residual	20	171.9			306.8			28	113			
Pooled									110			

environmental factor(s) exist that mediate the strength of predation risk differently among the study sites used by Trussell, Ewanchuk & Bertness (2002) and our study. At least four factors seem likely to explain site-specific differences in trait-mediated indirect interactions. First, differences in wave exposure may dilute the concentration of risk cues below a threshold concentration that *L. littorea* may require to be intimidated (Ferrari, Wisenden & Chivers 2010). The site where Trussell, Ewanchuk & Bertness (2002) conducted their study was sheltered (S. Hawkins, pers. comm.). This could explain a stronger effect size of predation risk there compared to our study, which was conducted at a shore of intermediate wave-exposure (M. Molis, unpubl. data). Similarly, the distance between *C. maenas* and prey was larger in the field than in the laboratory where the strength of predation risk effects was higher, fostering the possibility that cue dilution may lower strength of risk effects. The study by Freeman & Hamer (2009) corroborates this possibility as the effect of crab predation risk on dogwhelk foraging behaviour was lower in wave-exposed than in sheltered environments, suggesting that wave-exposure history can drive the effect size of trait-mediated indirect interactions. Second, the effects of predation risk may depend on prey density (Ferrari, Wisenden & Chivers 2010). The level of intimidation in *L. littorea* may perhaps decline with increasing periwinkle density because the individual risk of falling prey to a *C. maenas* should decrease for *L. littorea* as the number of conspecifics increases. The study by Edwards & Davies (2002) suggests that mucus trails of *L. littorea* contain some unknown cue(s). Trail-bound cues may provide information for a *L. littorea* specimen about the density of conspecifics. At the study site of Trussell, Ewanchuk & Bertness (2002), where crab predation risk influenced periwinkle foraging behaviour, periwinkle density was, on average, about seven times lower than at our study site, which may explain strong predation risk effects at their study site and weaker effects in our study. Third, differences in habitat heterogeneity may alter encounter rates between predators and prey, thereby changing predation risk. For instance, Lewis & Eby (2002) showed that predation risk for snails was reduced in intertidal saltmarsh habitats with complex structure. Furthermore, habitat heterogeneity and strength of predation risk can be interdependent in food chains where resources affect habitat structure. Trussell, Ewanchuk & Matassa (2008) demonstrated that the identity of resources can influence the degree of risk perceived by prey. By creating complex habitats, blue mussels increase refuge availability for dogwhelks from mollusc-eating crabs, by which dogwhelks experience a reduced predation risk. Fourth, the magnitude of predation risk effects may depend on resource availability (Preisser, Bolnick & Grabowski 2009). According to their meta-analysis, the non-consumptive effects of *C. maenas* should be stronger in habitats where changes in resources like seaweed recruits will vary dynamically in response to grazing by *L. littorea* than in habitats where resource availability would be independent of grazing. As seaweed recruits were not renewed in our study, the effect of predation risk should have been, with respect to a potential influence of resource dynamics, at least as strong as in the Trussell, Ewanchuk & Bertness (2002) study.

Despite short assay times, our study indicates for at least two reasons that *F. serratus* recruitment may benefit in the longer term from risk effects of nearby consuming *C. maenas*. First, risk cues have the potential to almost completely 'switch off' periwinkle consumption as indicated by the almost identical survivorship of *F. serratus* recruits in the presence and absence of periwinkles when nearby crabs consumed conspecific snails. Second, despite differences in the threat of real predation, risk effects showed no intraspecific variation. Thus, our study provides additional evidence about the causes by which non-consumptive predator effects can affect prey performance and indirectly survivorship of basal species to a greater extent than consumptive predator effects. Such examples on positive trait-mediated indirect effects on recruit survival of resources indicate that the persistence of basal species, like plants and seaweeds, may be to a larger extend top-down controlled than previously anticipated (*sensu* Peckarsky *et al.* 2008). The accumulating evidence that non-consumptive predator effects surmount their consumptive effects (e.g. Peacor & Werner 2001; Trussell, Ewanchuk & Matassa 2006b) provides insight into ecological mechanisms, e.g. on recruitment success of basal species under a high density of consumers. Thus, non-consumptive predator effects can facilitate the establishment and/or persistence of seaweed populations in hostile environments. Knowledge on facilitation in ecological processes is important for a comprehensive understanding for ecosystem functioning and structure (e.g. Bruno, Stachowicz & Bertness 2003). One ultimate consequence of positive indirect interactions between predators and resources are changes in the evenness and thus diversity and structure of communities as the number of survivors will increase in communities in which important consumers are affected by predation risk (Schmitz 2006). Consequently, our study suggests that interaction webs may provide more information than food webs about drivers of structure, function and perhaps stability of ecological communities.

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