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Detrital Subsidy to the Supratidal Zone Provides Feeding Habitat for Intertidal Crabs

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ABSTRACT: Beach-cast wrack of marine origin is considered a spatial subsidy to the marine-terrestrial transition zone. We found that the wrack line on sand and gravel beaches of Vancouver Island was frequented by intertidal purple shore crabs, *Hemigrapsus nudus* (Dana 1851) and densely colonized by detritivorous talitrid amphipods. Amphipods spend the day buried in sand and forage on beach wrack during the night. *H. nudus* were found in supratidal wrack patches immediately after nightly high tides in field censuses, but spent most of the day and ebb tides either submerged subtidally or hidden underneath intertidal rocks and boulders. In feeding trials, intertidal shore crabs were capable of preying on talitrid amphipods. We consider *H. nudus* an omnivore feeding on both fresh and decaying macroalgae as well as animal prey. Although living supratidally, amphipods were significantly preferred over intertidal littorine snails by foraging shore crabs. Handling time of amphipods was significantly shorter than for littorine snails. While amphipods had a reduced risk of predation by *H. nudus* when buried in the sand, foraging underneath wrack patches did not reduce predation pressure on amphipods by shore crabs. Rates of amphipod consumption by shore crabs were higher at darkness than daylight. In addition to an apparent day-night rhythm, tidal height and time elapsed since previous high tide had a significant influence on shore crab density within the wrack. We conclude that beach-cast wrack acts as a spatial subsidy by virtue of providing a valuable food source to talitrid amphipods, which are in turn consumed by shore crabs that ride the nightly high tide into supratidal wrack patches to reduce the risk of passing bare sand on their way to a feeding habitat rich in valuable prey.

Introduction

Beach-cast deposits of macroalgae and seagrass, termed wrack, function as important spatial subsidies (Polis et al. 1997) of organic material to sand and cobble beaches, especially in terms of providing a rich food source for a number of consumers (Pennings et al. 2000; Dugan et al. 2003). Owing to their high location on the beach platform, these beach-cast wrack deposits experience only very brief episodes of tidal inundation (cf., Orr et al. 2005). Semiterrestrial amphipods (Talitridae) are common detritivores in decomposing wrack deposits, often occurring at high densities (Griffiths et al. 1983; McLachlan 1985).

While it is well known that talitrid amphipods use wrack as a food source (Griffiths et al. 1983; Pennings et al. 2000), it remains an open question whether wrack patches effectively serve as shelter from potential predators (cf., Buck et al. 2003), as is known to be the case for aquatic amphipods (Norkko 1998; Vetter 1998; Corona et al. 2000). Amphipods resting and foraging underneath wrack patches would be hidden from visually-oriented predators, such as birds or small maritime mammals. Invertebrate predators relying on contact perception for prey capture, rather than visual cues (e.g., crabs or beetles), may be effective predators of amphipods in wrack patches, having access to amphipods during nocturnal hours, when amphipods are most active (Richards 1983).

In a series of studies on detrital subsidies to beaches in Barkley Sound (British Columbia, Canada), we observed dense populations of purple shore crabs (*Hemigrapsus nudus*) sheltered underneath high intertidal rocks within close proximity of wrack deposits in the supratidal beach zone. To access these supratidal wrack deposits as a potential food source, *H. nudus* must leave their shelter and move up the beach platform. The disadvantage of undertaking this potentially dangerous travel may be counterbalanced by the advantages of using wrack as a valuable feeding habitat.

The relatively weak claws of the generalist *H. nudus* impose restrictions upon their ability to feed on some intertidal animal prey (Behrens Yamada and Boulding 1998), since most animal prey available in the intertidal zone, such as *Littorina* spp., are hard-shelled and require substantial claw strength or handling periods. Wrack deposits contain high densities of calorie-rich talitrid amphipods (Griffiths

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*Corresponding author; tele: (+49) 431 880 4153; fax: (+49) 431 880 4747; e-mail: mzimmer@zoologie.uni-kiel.de et al. 1983; Creswell 1994), which can be easily crushed by the weak claws of *H. nudus*, owing to their soft exoskeletons.

Intertidal crabs are highly motile predators that exploit patches of high prey density; an attribute that permits exploitation of ephemeral prey patches (Behrens Yamada and Boulding 1996). Many crab species restrict feeding activity to certain intertidal zones or periods of tidal inundation (Robles et al. 1989). Crabs residing within the high intertidal zone experience reduced daily submersion time, significantly restricting the amount of tidally inundated foraging time. Foraging activity of intertidal crabs may also be highly dependent upon light levels (Dare and Edwards 1981; Robles et al. 1989). Many crab species exhibit diel cycles of activity with higher foraging activity during night (Marsden and Dewa 1994). Increased activity during night may dampen the risk of predation by visual-based, diurnal predators such as birds, fish, and maritime mammals. This combination of diel and tidal patterns may act in concert to regulate the daily foraging and activity patterns of intertidal crabs.

Despite the fact that *H. nudus* are among the most abundant intertidal crabs in coastal British Columbia, very limited information exists regarding their dietary habits and preferences. They are described as generalist herbivores mainly feeding on diatoms, desmids, and green algae (Behrens Yamada and Boulding 1998), but evidence of carnivory also exists (Dalziel and Boulding 2005). To shed more light on the feeding behavior and trophic status of such an abundant generalist feeder, we examine the movement of *H. nudus* to wrack patches, as well as their role as potential predators in these patches. We aim to prove that *H. nudus* are omnivorous feeders and elucidate potential animal prey items, determine if *H. nudus* access supratidal wrack deposits, and if so, under which tidal and diel circumstances, and test the hypothesis that supratidal talitrid amphipods can be used as a food source by *H. nudus*, and are even preferred over other potential food items of the intertidal area.

Materials and Methods

FIELD SAMPLING

Study Site

Field studies were conducted on a small, protected sand and gravel beach on the northeast corner of Edward King Island (48°52′01.56″N, 125°17′18.86″W), Barkley Sound, off the west coast of Vancouver Island (British Columbia, Canada). The study beach is approximately 75 m long and fringed on each side by large rock fields composed of cobbles and boulders. Dense populations of *H. nudus* reside within the rock fields. During each tidal cycle, a supratidal band of wrack is deposited among the rocks and along the entire length of the beach. A rich community of talitrid amphipods is found among the wrack, with *Megalorchestia pugettensis* (Dana 1853) and *Traskorchestia traskiana* (Stimpson 1857) being the most common amphipod species.

Night Transects

Beach-cast wrack was sampled for the presence of *H. nudus* on the nights of August 8 (4 d after neap tide), 15, and 22 (5 d before spring tide), 2003. Three transects were sampled per night, the survey of each being separated by a 2-h interval. The first transect per night coincided with the time of either the slack high or slack low tide after sunset and the overall sampling time (6 h) covered the entire interval of flood or ebb. Sample transects were established along the course of the wrack line. Quadrats of 0.5 × 0.5 m^2 were placed on the wrack line and all *H. nudus* within the quadrat were counted. Transect distance of 0 m was defined as the point where the beach wrack line met the bordering rock field. The first quadrat (= 1 m) was randomly placed between 0.5 and 1.5 m distance from the rock field; all subsequent quadrats were placed every 3 m along the wrack line. Since an undisturbed wrack line was essential for additional studies in another context, we were unable to determine the wrack by means of mass per area; percent cover of wrack within quadrat and minimum distance of rock shelter was recorded for each quadrat. The wrack within the rock field, where it is deposited more patchily and in larger amounts, was also sampled by means of 5 quadrats that were randomly placed within the area of wrack deposition in the rock field. Percent cover of wrack and number of crabs were recorded for each quadrat. Minimum distance to potential shelter within the rock field was defined as 0 m.

Day Transects

Daytime sampling followed the methods used for nocturnal sampling. A total of 4 diurnal transects were sampled on August 13 (9 d after neap tide) and 19 (8 d before spring tide), 2003. Because shore crabs are typically more active during diurnal high tides (Williams 1991; Marsdon and Dewa 1994), diurnal sampling was performed at high tides to maximize likelihood of finding *H. nudus* within wrack. This procedure biased our results towards higher crab densities during daytime, so that lower diurnal crab densities, relative to night, can be considered conservative.

LABORATORY EXPERIMENTS

Predators

Laboratory experiments were conducted at the nearby Bamfield Marine Sciences Centre. *H. nudus* of various size classes were collected by hand from underneath cobbles near the study site on Edward King Island. Crabs were held in seawater tanks with a constant flow of fresh seawater and abundant macroalgae (*Fucus* spp). Only crabs that had spent at least 24 h in the laboratory were used in experiments. Randomly chosen crabs were sexed, and the carapace width and the height of the propodite of the right chela were measured to the nearest millimeter (cf., Buck et al. 2003) before they were used in the experiments. Since claw size is related to food choice, we aimed at comparing *H. nudus,* which we consider an omnivore, with another grapsid crab, *Armases cinereum,* which has recently been shown to exhibit omnivorous feeding behavior (Buck et al. 2003).

Predation Trials

Predation trials with *H. nudus* were conducted in dry plastic tanks (30 × 17 cm^2). One randomly selected crab was placed in the tank along with 10 talitrid amphipods and 10 individuals of one of three littorine snails: *Littorina sitkana, L. scutulata,* or *L. subrotundata.* Each *Littorina* sp. was used in separate experiments, and a total of five trials were performed per species; no shelter was offered to prey organisms. Crabs and prey were left in darkness for 12 h per predation trial, and remaining prey items were counted at the conclusion of each trial. Dry tanks mimicked emersion at low tide and prevented *Littorina* spp. from climbing out of reach of crabs. *Littorina* spp. differ in shell thickness, with *L. sitkana* and *L. subrotundata* being lighter shelled (Dalziel personal communication). Only small *Littorina* (< 7 mm) were used to facilitate handling and crushing.

Previous feeding experiments have documented *H. nudus* predation on *L. sitkana* (Behrens Yamada and Boulding 1998). Additional feeding experiments were conducted with *L. sitkana* as the only prey item. One randomly selected crab was placed in a tank with 10 *L. sitkana.* Five trials were conducted for this experiment, using the same method as for the prey preference experiments.

Simultaneously, feeding trials (n = 10) in water-filled, lid-sealed plastic tanks (30 × 17 cm^2) with a continuous flow of fresh seawater yielded comparative data on overnight consumption of different subtidal and intertidal food items that enabled us to decide whether *H. nudus* acts as a detritivore, an herbivore, a carnivore, or an omnivore when submerged. For this, cobbles with known numbers of barnacles (mixed genera), 10 snails (*L. sitkana*), and known amounts of fresh and detrital *Fucus* cf., *gardneri* were placed in the tank before a randomly chosen crab was added. After 12 h, the numbers of barnacles and snails were counted, and algae were oven dried (24 h, 60°C) and weighed. The dry mass of the initial amount of algae was determined on the basis of a fresh mass:dry mass ratio for fresh and detrital *Fucus* (n = 15, each).

When several types of food are offered simultaneously, consumption of one cannot be assumed to be independent of consumption of the others. To avoid fallacies in statistical analyses of preference tests (cf., Peterson and Renaud 1989; Roa 1992; Manly 1993), all preference tests were statistically analyzed through randomization of data by using resampling statistics with 9999 iterations as implemented in the software poptools (http://www.cse.csiro.au/poptools/), since this approach incorporates such interdependencies. Fisher (1951) introduced permutation tests as a theoretical argument supporting Student's *t*-test, but this approach is also valuable for statistical tests in its own right (Bärlocher 1999). The repeated resampling of experimental data generates sets of artificial data. Instead of listing all possible arrangements, random arrangements of the original data are generated. By increasing the number of iterations, it can be decided whether the original experimental data deviate from a random distribution that would be expected if no preference was observed.

Protection from Predation

Effects of potential shelter on supratidal predator-prey interactions were tested in trials with *H. nudus* and amphipod prey overnight (n = 10, each). A single randomly chosen crab was placed in a plastic tank (30 × 17 cm^2) that was either bare, filled with 4 cm of moist sand, or filled with sand and a small patch of wrack that covered approximately 50% of the sand surface area. Prior to introducing the crab, 10 medium-sized talitrid amphipods were given time to acclimatize in the tank for 1 h. At the end of the experiment, crabs were removed, and the remaining amphipods were counted.

To compare nocturnal versus diurnal supratidal predation, plastic tanks (30 × 17 cm^2) were filled with 4 cm of moist sand. A circular bowl (10 cm diameter) containing seawater was sunk into the sand and a small rock shelter was constructed within the water bowl. Crabs were able to move freely between the water bowl and sand. A small pile of wrack was placed in the tank opposite the water bowl. Ten medium-sized talitrid amphipods were placed into the wrack pile. One randomly selected *H. nudus* (n = 5) was placed in the water bowl and either studied during daytime at 12 h of light or

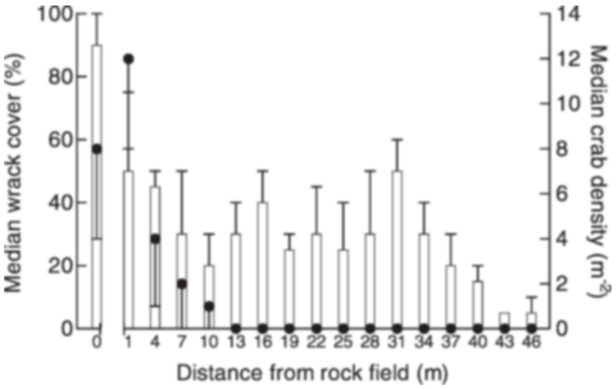

Fig. 1. Wrack cover (bars) and density of *Hemigrapsus nudus* (dots) underneath wrack along transects with increasing distance from shelter in an adjacent rock field. Crab density is not correlated with percent cover of wrack, but with distance from the rock shelter. Data are median ± median absolute deviation ($n = 9 = 3$ transects at 3 dates, each).

overnight at 12 h of dark. Amphipods remaining in the tank after 12 h were counted.

Prey Handling Time

To compare the time needed to handle a caught amphipod with the time needed for a hard-shelled snail (Behrens Yamada and Boulding 1998), we measured handling time of medium-sized amphipods for *H. nudus.* One randomly selected crab ($n = 10$) was placed in a dry, plastic tank with 10 amphipods. Crabs were watched by an observer under red light to minimize observer disturbance on crab behavior. Handling time was measured for only the first amphipod captured, beginning when the crab caught the amphipod and ending when the entire amphipod had been consumed.

Results

Daytime transects revealed an almost complete absence of *H. nudus* from beach wrack; in 80 diurnal quadrats sampled, only four individuals were found (0.05 crabs per quadrat) versus 97 individuals found at night ($n = 189$ quadrats: 0.5 crabs per quadrat). The distribution of *H. nudus* at nightly high tides was only marginally influenced by the percent cover of wrack (Fig. 1; Spearman $r_S = 0.409$, $n = 17$, $p > 0.06$), but was strongly influenced by both the distance from the rock shelter ($r_S = 0.803$, $n = 17$, $p < 0.001$) and tidal height (linear regression: $r^2 = 0.47$, $n = 9$, $p < 0.05$).

Observations in the field, both prior to and between transect samplings, indicated that initial movement of *H. nudus* into the wrack line coincided with the times of high tide maxima. At high tide, the water comes into close contact or even resuspends previously deposited wrack (Orr et al. 2005). The density of *H. nudus* within the wrack decreased significantly with time since previous high tide maxima (i.e., time since tide last transported crabs to wrack deposits; linear regression: $r^2 = 0.71$, $n = 9$, $p < 0.005$).

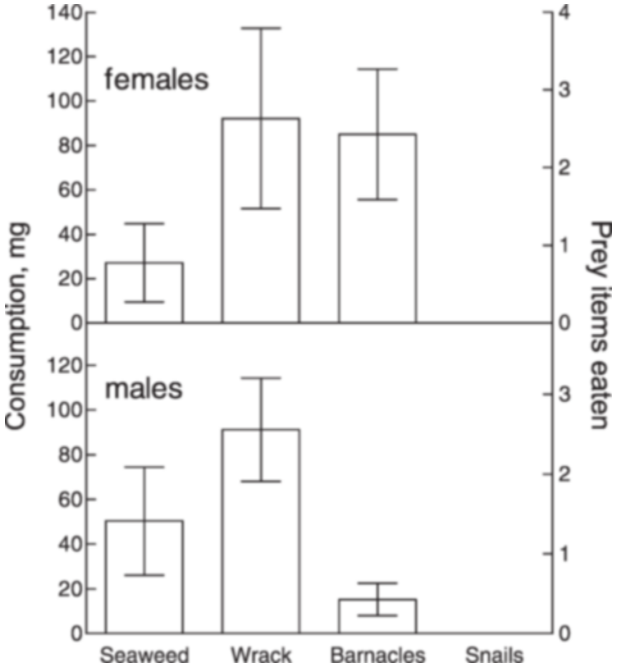

Fig. 2. Feeding preferences of submerged *Hemigrapsus nudus* when offered different food items simultaneously, indicating that shore crabs may act as omnivores. Females and males differ in their rates of barnacle consumption. Data are median ± median absolute deviation ($n = 9$).

During laboratory predation trials, submerged *H. nudus* fed on similar amounts of fresh and beach-tossed (wrack) *Fucus* sp. (Fig. 2; *U* test: $p > 0.8$), and preferred preying on barnacles (mixed genera) over preying on snails (*L. sitkana*; *U* test: $p < 0.001$). The absence of a preference between fresh and wracked seaweed suggests that the presence of decomposing seaweed alone does not explain *H. nudus* presence in beach-cast wrack; both fresh and wracked macroalgae are abundant in the intertidal zone. The consumption of both seaweed and barnacles confirms an omnivorous diet for *H. nudus.* When given a choice between amphipods and snails (*Littorina* spp.), emerged *H. nudus* always strongly preferred amphipods, irrespective of *Littorina* species (Fig. 3; *U* test: $p < 0.001$). In feeding trials with *L. sitkana* as the sole prey choice, no snails were consumed at all (data not shown).

In both sexes of *H. nudus,* claw size increased linearly with carapace width (males: $r^2 = 0.749$, slope $= 0.37 \pm 0.04$, $n = 24$, $p < 0.0001$; females: $r^2 = 0.664$, slope $= 0.25 \pm 0.04$, $n = 25$, $p < 0.0001$),

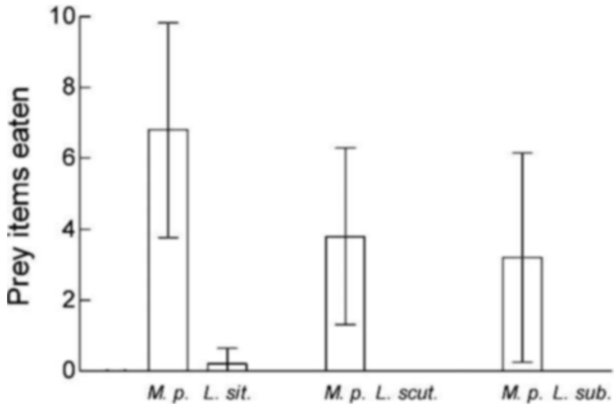

Fig. 3. Feeding preference of emerged *Hemigrapsus nudus* when offered talitrid amphipods (M. p. = *Megalorchestia pugettensis*) and different species of littorine snails (L. sit = *Littorina sitkana*, L. scut = *L. scutulata*, L. sub = *L. subrotundata*) simultaneously, indicating that soft-bodied amphipods are preferred over hard-shelled snails. Data are median ± median absolute deviation (n = 9).

but males had bigger claws than females of the same size (ANCOVA: $p < 0.001$). The difference increased with increasing body size, i.e., the regression coefficients were significantly different ($p < 0.01$), indicating that with increasing size males develop disproportionately larger claws than do females. Males differed from females in that they consumed fewer barnacles than females, perhaps because the smaller female claws facilitate pulling out the barnacle soft body from the hard carapace (Mews and Zimmer personal observation). Females (9 ± 1) and males (9 ± 1) did not differ from each other in how many amphipods (*M. pugettensis*) were consumed within the time provided during feeding tests (*U* test: $p > 0.9$).

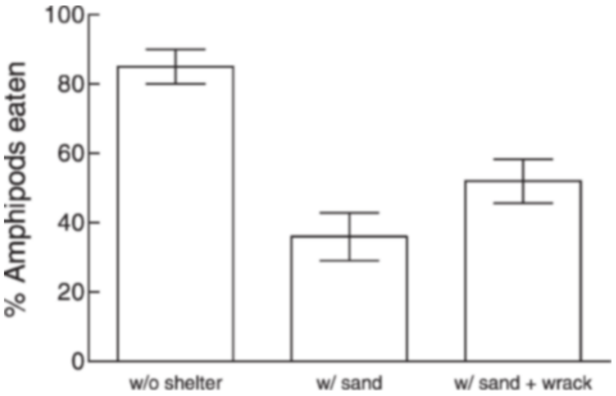

Fig. 4. Effect of sand (w/ sand) and additional wrack (w/ sand + wrack) on consumption of amphipods (*Megalorchestia pugettensis*) by *Hemigrapsus nudus* in comparison to shelter-free trials (w/o shelter), indicating that sand, but not wrack, provides protection from predation by foraging crabs. Data are median ± median absolute deviation (n = 9).

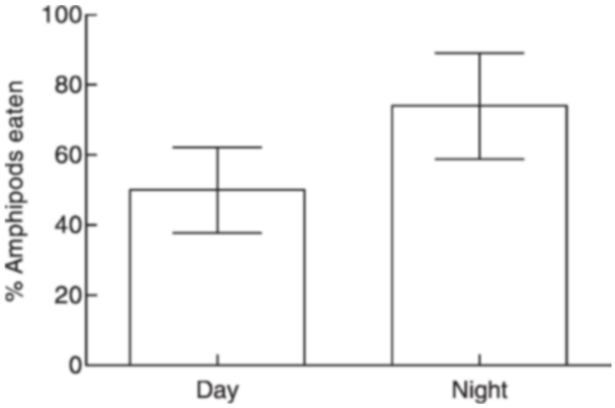

Fig. 5. Daytime and overnight consumption of amphipods (*Megalorchestia pugettensis*) by *Hemigrapsus nudus*, indicating higher consumption rates during night. Data are median ± median absolute deviation (n = 9).

Compared with shelter-free controls, sand significantly (ANOVA: $p < 0.001$) reduced predation on *Megalorchestia* by *H. nudus* (Fig. 4). Adding wrack only marginally resulted in a changed frequency of predation (ANOVA: $p > 0.07$), suggesting that wrack does not provide an effective shelter from predation. *H. nudus* consumed significantly more talitrid amphipods at night than during day (Fig. 5; *U* test: $p < 0.05$), consistent with the observation of higher *H. nudus* abundance in the nocturnal field transects.

From time of amphipod capture to complete consumption, *H. nudus* required 118 ± 8 s. This handling time for amphipods is approximately five times faster than values reported for *Littorina* snails (Behrens Yamada and Boulding 1998).

Discussion

The significant numbers of *H. nudus* within beach-cast wrack deposits during nightly high tides support our hypotheses that this intertidal crab may act as an omnivore and exits the water and travels up the beach gradient platform to forage underneath supratidal wrack patches rich in prey.

Clear diel patterns of *H. nudus* accessing wrack were observed. Observations at night revealed obvious crab movements out of the water and up the exposed beach towards the wrack line, while no crabs were observed moving or foraging out of the water during the day. Of the four diurnal transects, only four *H. nudus* were found in the wrack, indicating a 10-times lower density of emerged *H. nudus* during the day than during night. These few *H. nudus* were buried under a deep pile of wrack (ca. 25 cm) among the rock field, quite possibly using the wrack primarily as shelter. A complete diurnal data set with regards to tidal level would be necessary to draw more firm conclusions, but our present data conservatively confirm the essential absence of *H. nudus* from the supratidal wrack line during the day. Day and night simulated laboratory experiments provided good evidence regarding diel activity patterns. *H. nudus* consumed significantly more amphipods during simulated night than day, although they were still active and foraging during simulated day. Although these experiments may indicate increased nocturnal activity, laboratory conditions are admittedly limited. Foraging crabs only had to move short distances (ca. 15 cm) from water to wrack and had no tidal or crepuscular signals to cue movement. Nocturnal activity in beach wrack confers potential major advantages to *H. nudus*. Nocturnally foraging crabs are hidden in darkness from visually oriented terrestrial predators, and nighttime foraging coincides with maximal activity of talitrid amphipods that spend days mostly buried in sand (Richards 1983).

When given a choice, *H. nudus* foraging on land clearly preferred amphipods over littorine snails, which are highly abundant at the study site. *Littorina* spp. occupy the intertidal zone and could be efficiently preyed upon by crabs during times of tidal submersion, eliminating potentially dangerous foraging trips onto exposed flats. The handling time for an individual amphipod (ca. 2 min) was more than 6 min lower than the handling time for littorine snails (ca. 500 s) as reported by Behrens Yamada and Boulding (1998). This time-energetic benefit may be a major driving force prompting *H. nudus* movements to wrack deposits. When submerged, *H. nudus* preferred feeding on barnacles or *Fucus* wrack, and to some extent on fresh *Fucus*, rather than on littorine snails.

Another factor affecting feeding behavior of crabs may be claw size (Behrens Yamada and Boulding 1998). Males of the grapsid crab, *A. cinereum*, have bigger claws than females (Buck et al. 2003). Male *A. cinereum* eat more snails than females do, likely owing to their improved ability to crush shelled prey items. Both *A. cinereum* sexes prefer amphipods and isopods over snails (Buck et al. 2003). Although male *H. nudus* have bigger claws than females of the same size, feeding on talitrid amphipods did not differ between sexes; preying upon barnacles even appears to be facilitated by small claws. Allometric differences between sexes likely have other reasons than sex-specific prey selection in *H. nudus* and may simply be an evolutionary heritage rather than an adaptation to feeding habits.

In addition to an apparent day-night rhythm, tidal height and time elapsed since previous slack high tide appear to have the most significant influences on crab density within the wrack. The strong relationship between *H. nudus* density and time elapsed since previous high tide suggests that *H. nudus* ride the high tide into the wrack line. We propose that high tides contacting the wrack line may carry aqueous chemical signals from decomposing wrack to submerged *H. nudus*, providing a chemical cue that initiates travel to the wrack, but this hypothesis awaits experimental testing. Waiting for the slack high tide to access wrack would entirely minimize the travel distance between wrack and water. Concerning which portion of the wrack line will be used, the distance from rock shelter strongly dictates *H. nudus* distribution. The propensity of *H. nudus* to remain close to shelter in rock fields adjacent to the beach could preclude them from wrack access at larger beaches or areas lacking proper rock shelter. This observation could be an artifact of the study site, since abundant wrack deposits abutted rock fields at the study site, potentially eliminating the need for *H. nudus* to stray far from their daytime habitat.

It is unlikely that the movement of *H. nudus* to wrack patches is for shelter purposes alone, since adequate shelter is available under rocks in the intertidal zone, and reaching the wrack line might require movement over exposed areas of the beach. The presence of *H. nudus* within the wrack does not necessarily mean that amphipods are being used as a food source. The wrack itself may be fed upon (Griffiths et al. 1983), possibly being the main attractant for foraging crabs, while the occasional capture and ingestion of amphipods within wrack may be a secondary reason for movement into the wrack. We ruled this out, since *H. nudus* did not show any preference for feeding on wrack in laboratory trials, but did exhibit a clear preference for feeding on amphipods rather than other available prey. Owing to substantial amphipod densities (Griffiths et al. 1983; McLachlan 1985), shore crabs are likely encountering numerous amphipods when in the wrack. These encounters are potentially profitable feeding opportunities that may influence the decision of an individual *H. nudus* to access the wrack, and we hold that high densities of amphipods in supratidal wrack patches render them an attractive prey for *H. nudus*. The feeding habitat of talitrid amphipods is also a feeding habitat for their potential predators such as shore crabs (this study), rove beetles (Neame, Zimmer, Jelinksi, and Mews unpublished data), frogs (Orr personal communication), minks, and bears (Mews, Zimmer, and Jelinski personal observations).

The predators' effect on wrack decomposition by amphipods (Mews et al. 2006) may be substantial, but numerous studies indicate that increasing environmental structure reduces the ability of predators to capture prey (Gotceitas and Colgan 1989; Lewis and Eby 2002; Buck et al. 2003). While burying in the sand obviously provides some protection from predation by *H. nudus* to talitrid amphipods, foraging underneath wrack does not. Wrack did not significantly affect capture time of amphipods by the beach-dwelling rove beetle, *Thinopinus pictus* (Neame, Zimmer, Jelinski, and Mews unpublished data). Spending a significant amount of time within wrack patches appears to increase the risk of predation by predators that actively seek those wrack patches for foraging. We conclude that freshly deposited wrack, which becomes densely colonized by talitrid amphipods within less than one hour (Pelletier, Mews, Jelinski, and Zimmer personal observation), is more important to amphipods as a food source with suitable temperature and moisture conditions than as a shelter from predators.

Considering the available evidence, we deduce omnivorous feeding behavior of *H. nudus* that uses talitrid amphipods as a valuable food source. The abundant availability of these detritivores in wrack lines renders this supratidal subsidy a habitat worthy of intrusion for foraging. The risk of having to leave shelter, be it subtidally or underneath intertidal rocks and boulders, is minimized by nocturnal foraging at high tides. Because wrack lines are deposited at the previous high water mark, delaying foraging until high tide allows *H. nudus* to ride the tide into the wrack lines without having to pass exposed beach areas. As a next step, removal and addition of natural and artificial wrack in field experiments, as well as gut analyses of field collected crabs, may reveal direct evidence to corroborate or question our conclusions based on field observations and laboratory experiments.

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LITERATURE CITED

BÄRLOCHER, F. 1999. Biostatisik. Thieme, Stuttgart, Germany.

BEHRENS YAMADA, S. AND E. G. BOULDING. 1996. The role of highly mobile crab predators in the intertidal zonation of their gastropod prey. *Journal of Experimental Marine Biology and Ecology* 204:59–83.

BEHRENS YAMADA, S. AND E. G. BOULDING. 1998. Claw morphology, prey size selection and foraging efficiency in generalist and specialist shell-breaking crabs. *Journal of Experimental Marine Biology and Ecology* 220:191–211.

BUCK, T. L., G. A. BREED, S. C. PENNINGS, M. E. CHASE, M. ZIMMER, AND T. H. CAREFOOT. 2003. Diet choice in an omnivorous salt marsh crab: Different food types, body size and habitat complexity. *Journal of Experimental Marine Biology and Ecology* 292:103–116.

CORONA, A., L. A. SOTO, AND A. J. SANCHEZ. 2000. Epibenthic amphipod abundance and predation efficiency of the pink shrimp *Farfantepenaeus duorarum* (Burkenroad, 1939) in habitats with different physical complexity in a tropical estuarine system. *Journal of Experimental Marine Biology and Ecology* 253:33–48.

CRESWELL, P. J. 1994. Age dependent choice of redshank (*Tringa tetanus*) feeding location: Profitability or risk? *Journal of Animal Ecology* 63:589–600.

DALZIEL, B. AND E. G. BOULDING. 2005. Water-borne cues from a shell-crushing predator induce a more massive shell in experimental populations of an intertidal snail. *Marine Biology* 317:25–35.

DARE, P. J. AND D. B. EDWARDS. 1981. Underwater television observations on the intertidal movements of shore crabs, *Carcinus meanas*, across a mudflat. *Journal of the Marine Biological Association of the United Kingdom* 61:107–116.

DUGAN, J. E., D. M. HUBBARD, M. D. MCCRARY, AND M. O. PIERSON. 2003. The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. *Estuarine Coastal and Shelf Science* 58S:133–148.

FISHER, R. A. 1951. The Design of Experiments, 6th edition. Oliver and Boyd, Edinburgh, Scotland.

GOTCEITAS, V. AND P. COLGAN. 1989. Predator foraging success and habitat complexity: Quantitative test of the threshold hypothesis. *Oecologia* 80:158–166.

GRIFFITHS, C. L., J. M. E. STENTON-DOZEY, AND K. KOOP. 1983. Kelp wrack and the flow of energy through a sandy beach ecosystem, p. 547–556. *In* A. McLachlan and T. Erasmus (eds.), Sandy Beaches as Ecosystems. Junk, The Hague, The Netherlands.

LEWIS, D. B. AND L. A. EBY. 2002. Spatially heterogeneous refugia and predation risk in intertidal salt marshes. *Oikos* 96:119–129.

MANLY, B. 1993. Comments on design and analysis of multiple-choice feeding-preference experiments. *Oecologia* 93:149–152.

MARSDEN, I. D. AND R. S. DEWA. 1994. Diel and tidal activity patterns of the smooth shore crab *Cyclograpsus lavauxi*. *Journal of the Royal Society of New Zealand* 24:429–438.

MCLACHLAN, A. 1985. The biomass of macro- and interstitial fauna on clean and wrack-covered beaches in western Australia. *Estuarine, Coastal and Shelf Science* 21:587–599.

MEWS, M., M. ZIMMER, AND D. E. JELINSKI. 2006. Species-specific decomposition rates of beach-cast wrack in Barkley Sound, British Columbia, Canada. *Marine Ecology Progress Series* 328:155–160.

NORKKO, A. 1998. The impact of loose-lying algal mats and predation by the brown shrimp *Crangon crangon* (L.) on infaunal prey dispersal and survival. *Journal of Experimental Marine Biology and Ecology* 221:99–116.

ORR, M., M. ZIMMER, D. E. JELINSKI, AND M. MEWS. 2005. Wrack deposition on different beach types: Spatial and temporal variation in the pattern of subsidy. *Ecology* 86:1496–1507.

PENNINGS, S. C., T. H. CAREFOOT, M. ZIMMER, J. P. DANKO, AND A. ZIEGLER. 2000. Feeding preferences of supralittoral isopods and amphipods. *Canadian Journal of Zoology* 78:1918–1929.

PETERSON, C. H. AND P. E. RENAUD. 1989. Analysis of feeding preference experiments. *Oecologia* 80:82–86.

POLIS, G. A., W. B. ANDERSON, AND R. D. HOLT. 1997. Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28:289–316.

RICHARDS, L. J. 1983. Feeding and activity patterns of an intertidal beetle. *Journal of Experimental Marine Biology and Ecology* 73:213–224.

ROA, R. 1992. Design and analysis of multiple-choice feeding-preference experiments. *Oecologia* 89:509–515.

ROBLES, C., D. A. SWEETNAM, AND D. DITTMAN. 1989. Diel variation of intertidal foraging by *Cancer productus* L. in British Columbia. *Journal of Natural History* 23:1041–1049.

VETTER, E. W. 1998. Population dynamics of a dense assemblage of marine detritivores. *Journal of Experimental Marine Biology and Ecology* 226:131–161.

WILLIAMS, B. G. 1991. Comparative studies of tidal rhythms - V. Individual variation in the rhythmic behaviour of *Carcinus maenas* (L.). *Marine Behaviour and Physiology* 19:97–112.

SOURCES OF UNPUBLISHED MATERIALS

DALZIEL, B. personal communication. Department of Zoology, University of Guelph, Guelph, ON N1G 2W1, Canada.

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