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ORIGINAL PAPER

Swarms of swift scavengers: ecological role of marine intertidal hermit crabs in California

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Abstract While marine hermit crabs are well known for being omnivorous filter feeders, less is known about the role they may play as active carrion scavengers in intertidal ecosystems. Prior studies have revealed that intertidal hermit crabs can be attracted to chemical cues from predated gastropods. Yet their attraction is usually assumed to be driven primarily by the availability of new shells rather than by food. We conducted field experiments to assess hermit crabs' potential role as generalist carrion scavengers on the California Coast, examining their speed of attraction and the size of the aggregations they formed in response to chemical cues from freshly smashed gastropods and mussels, both of which indicated available carrion. Compared to all other marine species, hermit crabs (*Pagurus samuelis*, *P. hirsutiusculus*, and *P. granosimanus*) were the fastest to arrive at the provisioning sites. Hermit crabs also dominated the provisioning sites, accumulating in the largest numbers, with aggregations of up to 20 individuals, which outcompeted all other scavengers for carrion. Notably, hermit crabs arrived equally quickly for both smashed gastropod and mussel, even though the latter does not offer suitable shells for hermit crabs and even though the former only yields shell-related chemical cues over time frames longer than our experiments. These results thus suggest that shell availability is not the only, or even the primary, reason marine intertidal hermit crabs aggregate at carrion sites; they also aggregate to forage, thereby playing an important role as active carrion scavengers in intertidal ecosystems.

Introduction

Tide pools within the rocky intertidal boast exceptionally high levels of biodiversity as well as some of the strongest levels of physical disturbance of any habitat (Denny and Gaines 2007). Ocean waves crashing on rocky shores routinely move at speeds of more than 5 m/s (Gaylord 1999), generating powerful hydrodynamic forces that can dislodge even well-anchored organisms (Denny et al. 1998; Gaylord et al. 2001). Intertidal wave action can also shift rocks and other heavy materials, putting organisms at risk of being smashed in spite of their protective shells and armored exteriors (Vermeij 1993). As a consequence, carrion is frequently produced in tide pools within the rocky intertidal, both through abiotic forces like wave action and through biotic forces like shell-crushing predators (Vermeij 1993). Many species rely on such carrion 'casualties' and the trophic transfer of nutrients they provide (King et al. 2007). However, the availability of fresh carrion is unpredictable (Britton and Morton 1994), and therefore, the most effective scavengers must be able to quickly locate and dominate

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Table 1 Wilcoxon signed-rank tests comparing the number of each organism at the end of the control period ($t = 0$ min) versus the end of the experimental period ($t = +10$ min)

	Experimental condition			
	Gastropod smashed	Gastropod live	Mussel smashed	Mussel live
Hermit crabs	**$T = 3, p < 0.0001$, ES = 0.947**	$T = 102, p = 0.874$	**$T = 4, p < 0.0001$, ES = 0.944**	$T = 75, p = 0.312$
Gastropods	$T = 87, p = 0.497$	$T = 96, p = 0.604$	$T = 77, p = 0.386$	$T = 89, p = 0.574$
Brachyuran crabs	$T = 104, p = 0.510$	$T = 105, p = 0.492$	$T = 96, p = 0.514$	$T = 96, p = 0.507$
Gobies	$T = 105, p = 0.566$	$T = 86, p = 0.465$	$T = 86, p = 0.500$	$T = 96, p = 0.559$

$N = 20$ for each condition. To break ties and deal with zeroes in the data, we randomly altered counts by 0.001 in either direction. This process was repeated 1000 times and the average V statistic and p value reported. Effect sizes are listed where significant effects occurred

Bold designates a statistically significant effect

new carrion resources. What species show such behavioral specializations for a scavenging lifestyle in tide pools?

Of the many organisms that inhabit tide pools, crustaceans exhibit acute chemosensory abilities (reviewed in Breithaupt and Theil 2011). As such, many crustaceans can quickly locate the scent of carrion and orient to this valuable food source. As crustaceans, hermit crabs (Decapoda, Anomura) share these fine chemosensory abilities (Gherardi and Tricarico 2011), and their mobility and abundance in tide pools make them excellent candidates as carrion scavengers (Holling 1957; Britton and Morton 1994). Intertidal hermit crabs, however, are primarily considered microphagous detritivores (Reese 1969; Kunze and Anderson 1979; Hazlett 1981; Rittschof 2007) and are thought to only scavenge for carrion as a secondary foraging strategy (Schembri 1982). Surprisingly, little empirical work has actually assessed hermit crabs' effectiveness as carrion scavengers or has compared them with other sympatric intertidal species. Indeed, as Hazlett (1981, p. 1) noted on the first page of his review of hermit crab behavior, still authoritative after over three decades: "Most ecological studies have focused completely on the crab–shell interaction, and relatively little work has been done on the crabs as an element of marine ecosystems." Consequently, relatively little is known about the feeding ecology of many hermit crabs (Bertness 1981; Hazlett 1981; Tran 2013; Laidre 2013a), so their potential role as active scavengers in intertidal ecosystems has yet to be fully addressed.

Pioneering experiments by McLean (1974) and Rittschof (1980a) highlighted hermit crabs' attraction to simulated predation sites involving the scent of killed gastropods. An ability to quickly locate gastropod predation events may aid hermit crabs in finding new shells, since many predators leave shells intact after consuming the gastropod's flesh (reviewed in Table 1 of McGuire and Williams 2010). It has therefore been argued (Rittschof 1980b, 1992; Rittschof et al. 1992; Mclean 1983; Gilchrist 1984; Pezzuti et al. 2002; Tricarico and Gherardi 2006; Tricarico et al. 2009) that hermit crabs are attracted to the scent of gastropod flesh primarily, if not exclusively, because it serves as an indicator of shell availability. Critically though, the attractants in gastropod flesh that indicate shell availability are only released an hour or more after a gastropod is smashed; or if the gastropod flesh is treated with predator proteases like trypsin, which generates small peptides that serve as 'shell cues' (Rittschof 1980b). In contrast, carrion from non-gastropod sources or carrion from freshly smashed gastropod that is less than 1 h old (and has not been treated with proteases) should only be attractive to hermit crabs as food, since such carrion does not provide shell-related cues. Are hermit crabs attracted to such non-shell carrion?

Interestingly, laboratory studies have demonstrated that despite the absence of shell cues, fresh gastropod carrion as well as other types of non-gastropod carrion can sometimes be attractive to hermit crabs (Tricarico et al. 2011). Additionally, both laboratory and field observations have suggested that even when crabs are attracted to carrion from gastropods, they may show an interest not just in entering a new shell but also in consuming the flesh remaining within the shell (Laidre 2011). Notably, some predators do not leave gastropod shells intact or suitable for occupation by hermit crabs (Vermeij 1993), even though a by-product of their predation may be strong chemical 'shell cues' indicative of gastropod death. Thus, even the scent of gastropod flesh that is more than an hour old will not always be predictive of newly available shells. And yet hermit crabs might still benefit from being attracted, given the value of carrion itself as a protein-rich food source worth fighting over (Britton and Morton 1994; Laidre 2007). Hermit crabs might therefore fulfill an important ecological role within marine ecosystems if their scavenging extends beyond searching for shells. Is there any evidence that hermit crabs fulfill such a generalist foraging role?

In the laboratory, hermit crabs signal and fight intensely for mussel (Laidre 2007; Laidre and Elwood 2008), a carrion source that is not associated with a suitable shell home for hermit crabs. And in the wild, a limited number of field experiments have suggested that hermit crabs can be highly motivated for other non-gastropod carrion. Specifically, Ramsay et al. (1997) deployed an underwater video camera to film scavengers that were experimentally attracted to dead fish bait dropped into the sub-tidal. Only two trials were conducted, but in both trials, hermit crabs (*Pagurus bernhardus*) were the fastest scavengers to arrive at the site, forming the largest aggregations of any species, and remaining at the site for extended periods to fight for and feed on the carrion. Similarly, Scully (1983) reported a single trial involving a crushed mussel in the intertidal and found that nearly 100 hermit crabs (*Pagurus longicarpus*) swiftly swarmed to and dominated the site within minutes. Both these preliminary reports deserve more systematic follow-ups, with a larger number of trials.

Here, we examined the potential role of hermit crabs as scavengers based on their attraction to fresh carrion that lacked any associated 'shell cues.' Our experiments tested the attractive value of two types of carrion, gastropod and mussel carrion. Mussel does not provide a suitable shell for hermit crabs, so when smashed, it should be attractive only as an eatable carrion source. Likewise, because we provided both the mussel and the gastropod carrion immediately after smashing live specimens, we ensured that there were no shell cues associated with the gastropod carrion. Our experiments thus revealed how strongly hermit crabs were attracted to carrion that was purely indicative of food rather than shells. We incorporated controls for each carrion type and structured our observations to reveal the total number of crabs that aggregated (the size of their 'swarm') as well as the temporal dynamics over which they were attracted (how 'swiftly' they arrived). Moreover, we compared hermit crabs' attraction to the carrion with that of sympatric species to measure hermit crabs' relative importance as scavengers within the ecosystem. Our experiments therefore allowed us to ask whether intertidal hermit crabs perform an important ecological role, acting as swarms of swift scavengers that converge to feed on intertidal carrion more quickly and in greater abundance than other species.

Methods

Study site and species

We conducted our experiments in the Pacific intertidal off the coast of California, an area renowned for its biodiversity (Morris et al. 1980). Prior field experiments on hermit crabs' attraction to simulated predation sites have, for the most part, been conducted in the Atlantic Ocean (Rittschof 1980a; Tricarico and Gherardi 2006) and the Mediterranean Sea (Tricarico et al. 2009), so our study provides valuable comparative data from the Pacific. Observations and experiments were carried out in the rocky intertidal habitat outside the Bodega Marine Laboratory (Figure S1), located on the Bodega Marine Reserve in Sonoma County. This area boasts California's northernmost exposure of coastal granitic rock, which has been carved out by wave action to produce a complex mosaic of tide pools. A rich community of marine species inhabits this area of rocky intertidal, including: (1) three species of hermit crabs (*Pagurus samuelis, P. hirsutiusculus*, and *P. granosimanus*; Bollay 1964); (2) a variety of species of shelled mollusks, with the California mussel (*Mytilus californianus*) being especially abundant, and with the black turban snail (*Chlorostoma funebrale*, previously classified as *Tegula funebralis*) being the most abundant gastropod; (3) many species of brachyuran crabs (including members of the *Pugettia, Scyra, Cancer, Lophopanopeus, Pachygrapsus,* and *Hemigrapsus* genera); and (4) several species of gobie (Gobiidae) (Morris et al. 1980). Carrion produced in this area of the intertidal is thus potentially available to many species.

During preliminary observations, we found hermit crabs aggregated around and feeding on a variety of naturally produced carrion, including non-gastropod carrion such as mussel, jellyfish, and brachyuran crab claws (Laidre and Greggor, personal observation). These observations motivated a series of experiments examining carrion scavenging by hermit crabs and other tide pool inhabitants.

General experimental protocol

To investigate hermit crab carrion scavenging, we conducted 100 experiments, 80 described in this section and another 20 described in the next section. For 80 experiments, we provisioned tide pools with either a gastropod (*C. funebrale*) or a mussel (*M. californianus*). Of these 80 experiments, 20 each were conducted using (1) a live gastropod (control), (2) a gastropod killed by smashing, (3) a live mussel (control), or (4) a mussel killed by smashing. Local rocks were used to smash the gastropods and mussels. All experiments were conducted during daylight at low tide, spanning February to July 2011. The experimental condition (gastropod or mussel, live or smashed) was randomly allocated.

Each experiment involved the same core design and set of steps. First, the experimenter (either A.G. or M.L.) located a tide pool. Most tide pools at the study site have lengths and widths between 1 and 3 m. We found a flat area within the tide pool that was open to observation and not obscured by seaweed. We then set down a quadrat (14.5 × 14.5 cm) composed of black wire. This quadrat was used to demarcate the focal area immediately surrounding where the stimulus (gastropod or mussel) was eventually introduced. After placing the quadrat, the experimenter moved to the edge of the tide pool and observed for several minutes to confirm that hermit crabs were present within

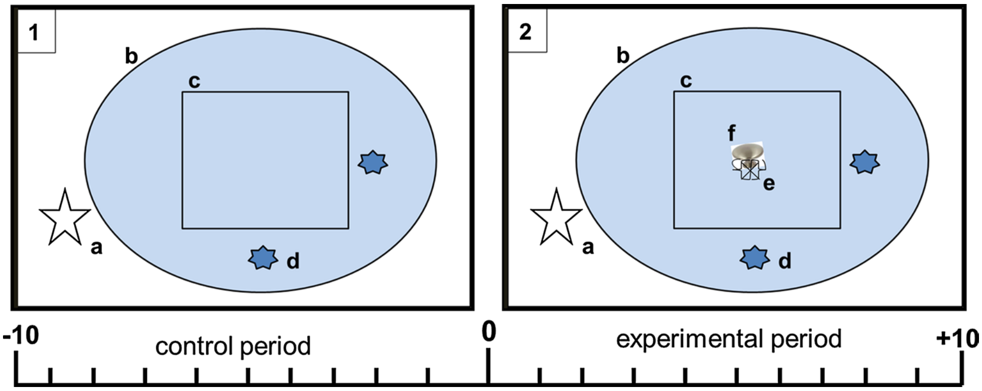

Fig. 1 **1** Conditions necessary for experiment to begin, with timeline below showing 10-min control period and **2** time at which experimental stimulus was dropped in (at $t = 0$ min), with timeline below showing 10-min experimental period. *Icons* represent (*a*) experimenter, (*b*) tide pool, (*c*) quadrat, (*d*) hermit crab, (*e*) mesh with experimental item, and (*f*) weight

the pool. If there was at least one hermit crab on two or more sides of the quadrat, then the experimenter remained in position and began an experiment (Fig. 1). Throughout the experiment, the experimenter remained stationary while observing the quadrat from above.

Each experiment lasted 20 min, the design paralleling experiments in terrestrial hermit crabs by Laidre (2010, 2013b). During the first 10 min (from $t = -10$ to $t = 0$ min), we collected baseline data on the number of hermit crabs and any other macroscopic scavengers (gastropods, brachyuran crabs, and gobies) that we observed in the quadrat at 1-min intervals. During this control period, no materials had yet been placed inside the quadrat, so the data indicate the general background activity within the tide pools. At the end of the control period ($t = 0$ min), the experimenter extended his or her arm above the quadrat and dropped a set of prepared materials (detailed below) into the center of the quadrat. This arm movement and the materials that were dropped in typically caused nearby hermit crabs to temporarily duck in their shells, but only temporarily. Usually within seconds, crabs and other organisms emerged and resumed their prior behavior. Once the materials had been dropped into the quadrat, initiating the experimental period, we recorded the same data (on the number of crabs and other species present in the quadrat) for another 10 min (from $t = 1$ to $t = +10$ min) at 1-min intervals. We noted the exact time (to the nearest second) that an organism (hermit crab or other) first initiated contact with the dropped in item. If the organism that first made contact was not a hermit crab, then we also noted when the first hermit crab subsequently made contact with the item. Since it was not possible to readily differentiate the three hermit crab species from overhead (and all were present in the quadrats at the end of our experiments on multiple occasions), we grouped them together in our count.

The materials that were dropped into the quadrat (gastropod or mussel, whether live or smashed) were wrapped in black rubber mesh that was tied with thin wire and weighted down with a metal weight (100 g). The mesh allowed carrion chemical cues to emanate and also allowed scavengers to pick at available carrion while still keeping the specimen (whether live or smashed) consolidated. The metal weight anchored the materials inside the quadrat, so that attraction to the bait could be readily observed. We collected the mussel or gastropod specimen immediately prior to each experiment, preparing the materials to be dropped in during the 10-min control period and then smashing the specimen (if it was to be killed) immediately before $t = 0$ min. Mussel and gastropod specimens were chosen such that the raw amount of flesh they contained was approximately equal: The mussels, with their elliptical shape, were chosen with lengths of 2–3 cm, while the gastropods, with their more globular shape, were chosen with lengths and heights of 1–2 cm.

At the end of each experiment, the quadrat, the attached weight, and the experimenter's hands were all washed thoroughly in seawater before beginning the next experiment, thus eliminating any residual odor from the prior experiment. New mesh and new wire were used for each experiment. Individual tide pools were only tested once per day, and on subsequent test days, we targeted our experiments in different broad sections of our study site (see Figure S1) to avoid re-testing the same tide pools. In the few cases where some tide pools might possibly have been re-tested at a later date, at least several days (and up to 30 days) had passed since these pools were last tested—and thus the highly mobile inhabitants in these pools, like hermit crabs, had almost certainly changed.

Extended experiments

An additional set of 20 extended experiments were conducted using the same core design as described above, with a lengthened experimental period that lasted for 30 min after the materials were dropped into the tide pool. These experiments all used smashed mussel and were undertaken to determine whether the number or composition of scavengers inside the quadrat varied over longer periods.

Analyses and predictions

We tested the effect of each of the four conditions (gastropod smashed, gastropod live, mussel smashed, and mussel live) on the number of hermit crabs and other attendants attracted to the quadrat and on the speed with which contact was first made. All data analyses were conducted in R (R Core Team 2012). For data that was non-normally distributed, we first tried transforming the data and otherwise used nonparametric tests.

We predicted that if edible, non-shell carrion is attractive to hermit crabs, then the number of hermit crabs within the quadrat would significantly increase from the control period to the experimental period in both the gastropod smashed and mussel smashed conditions, but not in the two control conditions (gastropod live and mussel live). To test this prediction, we compared the final sample point during the control period ($t = 0$ min) with the final sample point during the experimental period ($t = +10$ min). The means for each of these sample points, across all experiments of a given condition, were compared using a Wilcoxon signed-rank test (a nonparametric equivalent to a paired t test), since data were not always normally distributed. We also conducted a separate analysis in which we compared (1) the average number of crabs in the quadrat during the 10 sample points in the control period ($t = -10$ to $t = -1$ min) with (2) the average number of crabs in the quadrat during the 10 sample points in the experimental period ($t = +1$ to $t = +10$ min). The 10 counts made during each of these two periods were then averaged and the means across all experiments were compared with a Wilcoxon signed-rank test. Ultimately, we obtained similar results from both these different analyses, aside from one exception. In the Results section, we therefore report the one exception and otherwise only detail our analyses based on comparing the final two sample points.

If both gastropod and mussel carrion, in general, is attractive to hermit crabs, then we predicted that there would be no significant difference between the gastropod smashed condition and the mussel smashed condition, either in the number of hermit crabs that accumulated in the quadrat or in the speed with which hermit crabs first arrived and contacted each type of carrion. We tested this prediction by examining the number of hermit crabs in the final sample point ($t = +10$ min) for the gastropod smashed and mussel smashed conditions and by examining when hermit crabs first touched each type of carrion.

All the tests described above were also carried out for every species besides hermit crabs that was counted inside the quadrat. We predicted that if hermit crabs fulfill an important scavenging role compared to other organisms in the intertidal, then hermit crabs would show a significant increase in response to carrion, whereas other organisms would not. We also predicted that if hermit crabs are not just scavengers but are also swift scavengers, then they would consistently be the first organism to make contact with the carrion after it was dropped into the quadrat. We report the times that hermit crabs first arrived and contacted each carrion source.

Finally, to test whether the number or composition of scavengers varied over longer time periods, we compared the scavengers present in the quadrat at the end of the normal-length experiments ($t = +10$ min) versus the end of the longer experiments ($t = +30$ min), both of which involved smashed mussel.

Figures in the results show the counts of hermit crabs made at each 1-min sample point across the entire experiment (from $t = -10$ to $t = +10$ min), documenting the temporal dynamics of hermit crabs' numbers within the quadrat.

Results

Increase in hermit crab numbers

Hermit crabs were strongly attracted to the carrion in the gastropod smashed and mussel smashed conditions, with their numbers rising steeply across the experimental period (Fig. 2). In particular, hermit crabs increased significantly in the quadrat between the end of the control period and the end of the experimental period for both conditions (Wilcoxon signed-rank tests; smashed gastropod: $T = 3$, $N = 20$, $p < 0.0001$; smashed mussel: $T = 4$, $N = 20$ $p < 0.0001$; effect sizes for both conditions were large; Table 1). No such increase in the number of hermit crabs occurred for either the gastropod live or the mussel live condition (Wilcoxon signed-rank test; gastropod live: $T = 102$, $N = 20$, $p = 0.874$; mussel live: $T = 75$, $N = 20$ $p = 0.312$). When the analysis included all sample points (rather than just the two at the end of the control and experimental period), then in the mussel live condition, there was a significant (but minor) increase in the number of hermit crabs between the control and experimental period (compare Tables 1, 2).

In addition to accumulating in number within the quadrat, hermit crabs were also significantly more likely to contact the smashed gastropod and mussel conditions compared to the live gastropod and mussel conditions (Fisher's exact test: $p < 0.001$; Fig. 3a).

Attraction to gastropod versus mussel

The smashed gastropod and mussel conditions appeared equally attractive to hermit crabs: There was no difference between these conditions in the number of hermit crabs that

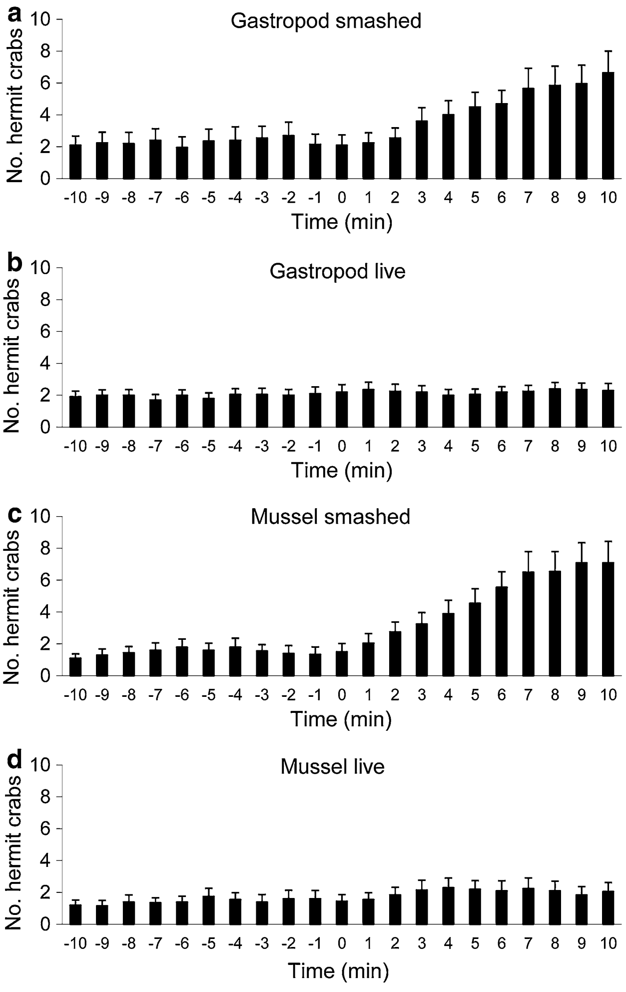

Fig. 2 Number (mean + SE) of hermit crabs present within the quadrat during each minute of the experiment. At $t = 0$ min, the experimental stimulus was dropped into the tide pool. $N = 20$ trials for each condition: **a** gastropods that were smashed, **b** gastropods that were live, **c** mussels that were smashed, and **d** mussels that were live

accumulated at the end of the experimental period (Mann–Whitney *U* test; $U = 19.93$, $N_1 = 20$, $N_2 = 20$ $p = 0.604$; compare Fig. 2a vs. c). Nor was there a difference in the speed with which hermit crabs first made contact with either type of carrion (data log transformed, *t* test; $t_{35} = 0.1367$, $p = 0.89$; Fig. 3b).

Hermit crabs versus other organisms

In contrast to the results for hermit crabs, no other organisms showed a significant change in abundance between the control and experimental period for any of the conditions (Table 1; Figures S2–S4). Moreover, hermit crabs were consistently the first organism to make contact with both the gastropod and the mussel, whether it was provided smashed or live: Of our $N = 80$ experiments, in $N = 58$ experiments an organism successfully contacted the item within 10 min of our dropping it in, and in all but one of those instances, the organism making first contact was a hermit crab. Hermit crabs first contacted the smashed gastropod in 2.90 ± 2.23 min (mean ± SD) and the smashed mussel in 2.87 ± 2.47 min.

Aggregation size over time

The size of hermit crabs' aggregations did not change when they were given three times longer to aggregate: No significant difference existed in the number of hermit crabs 10 min after compared to 30 min after the smashed mussel was dropped in (Mann–Whitney *U* test: $U = 32.34$, $p = 0.395$; Fig. 4). Hermit crabs thus reached peak aggregation size relatively quickly in response to carrion.

Discussion

Shells represent an important resource for hermit crabs' reproductive success (Hazlett 1981). However, shells are not the only resource that matters for hermit crabs (Schembri 1982; Ramsay et al. 1997; Laidre 2011; Tran 2013; Tran et al. 2014). Like other organisms, hermit crabs must acquire enough food to fuel growth and survival. Carrion

Table 2 Wilcoxon signed-rank tests comparing mean abundance across the entire control period ($t = -10$ to -1 min) versus the entire experimental period ($t = +1$ to $+10$ min)

	Experimental condition			
	Gastropod smashed	Gastropod live	Mussel smashed	Mussel live
Hermit crabs	**$T = 7, p < 0.0001$, ES = 0.887**	$T = 79, p = 0.340$	**$T = 3, p < 0.0001$, ES = 0.970**	**$T = 47, p = 0.030$, ES = 0.42**
Gastropods	$T = 70, p = 0.286$	$T = 91, p = 0.621$	$T = 72, p = 0.285$	$T = 98, p = 0.759$
Brachyuran crabs	$T = 95, p = 0.514$	$T = 104, p = 0.522$	$T = 91, p = 0.499$	$T = 103, p = 0.512$
Gobies	$T = 93, p = 0.582$	$T = 79, p = 0.391$	$T = 88, p = 0.488$	$T = 88, p = 0.514$

$N = 20$ for each condition. To break ties and deal with zeroes in the data, we randomly altered counts by adding small amounts of noise (around 0.001) in either direction. This process was repeated 1000 times and the average V statistic and *p* value reported. Effect sizes are listed where significant effects occurred

Bold designates a statistically significant effect

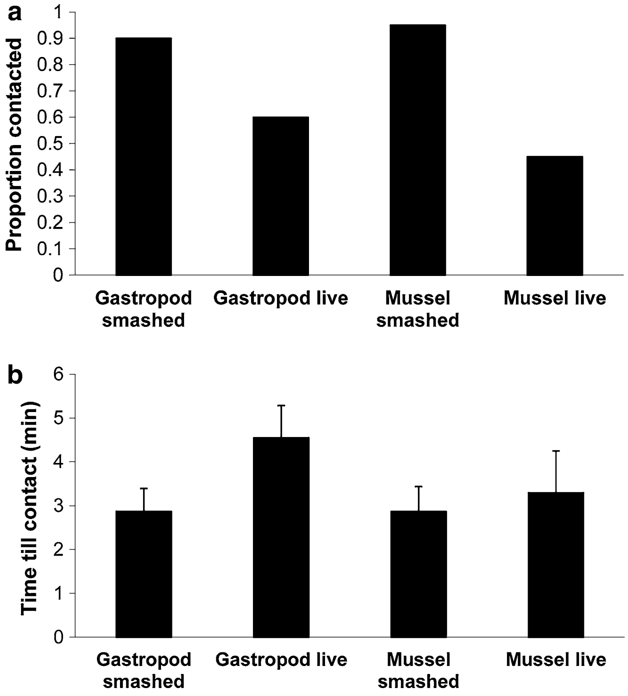

Fig. 3 **a** Proportion of trials in which hermit crabs contacted the experimental stimulus ($N = 20$ trials for each condition). **b** Time (mean + SE) till hermit crabs contacted the experimental stimulus, calculated from when the stimulus was dropped into the tide pool at $t = 0$ min ($N = 18$ for gastropod smashed, $N = 12$ for gastropod live, $N = 19$ for mussel smashed, and $N = 9$ for mussel live, since the stimulus was not contacted in all $N = 20$ experiments)

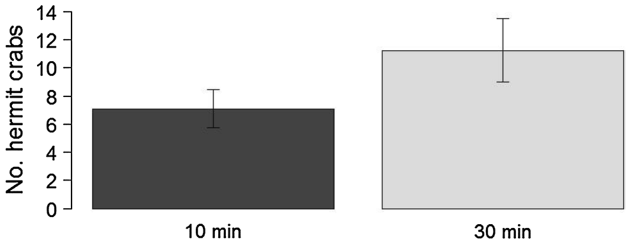

Fig. 4 Number (mean + SE) of hermit crabs that accumulated at 10 versus 30 min after the mussel smashed condition

may, therefore, represent a critical food resource for hermit crabs, especially in the intertidal, where high levels of abiotic and biotic disturbance frequently result in organisms being either smashed by waves (Denny et al. 1998; Gaylord 1999, 2007; Gaylord et al. 2001) or crushed by predators (Vermeij 1987, 1993).

In the present study, we simulated carrion production in the intertidal by smashing shell-bearing organisms (gastropods and mussel) that live sympatrically with hermit crabs. We found that hermit crabs were strongly attracted to this carrion, even though neither carrion source was associated with shell cues and thus only indicated a potential food resource. Our results thus suggest that marine intertidal hermit crabs are not solely attracted to scents that indicate shell availability, so at least in some populations, hermit crabs are highly motivated for carrion consumption (Scully 1983; Ramsay et al. 1997). Similar attraction to smashed mussel and other carrion occurs in intertidal hermit crabs in Northern Ireland (*Pagurus bernhardus*) and in Costa Rica (*Clibanarius albidigitus* and *Calcinus obscurus*) (Laidre, personal observation). Our results contrast with some other studies that have provisioned carrion to hermit crabs (e.g., Rittschof 1980a; Gilchrist 1984; Bozzano and Sarda 2002), which found that hermit crabs are only attracted to gastropod carrion once it begins to emanate peptides, which act as shell cues. What could account for these divergent results?

Different populations of hermit crabs may experience varying degrees of food versus shell limitation, with some areas having a more reliable supply of food and some having a more reliable supply of shells (Hazlett 1981; Barnes and De Grave 2000). Spatial heterogeneity in food or shell availability could therefore account for the differences between studies that have examined hermit crabs' motivation for carrion with versus without shell cues. Interestingly, even within the same population, hermit crabs' relative motivation for eatable carrion versus carrion that is also indicative of shells could change dramatically across time due to large-scale ecological events, like red tides (Prezelin 2007). Such events may kill vast numbers of gastropods, while leaving their shells intact, thereby generating a temporarily surplus of shells in the hermit crab housing market and increasing the importance of carrion as a source of food to fuel growth. Additionally, if crabs are satiated before being offered chemical cues (e.g., Gherardi and Atema 2005), then their attraction to food-related cues would likely lessen. Further comparative studies across hermit crab species, as well as studies focusing on single-hermit-crab populations during temporally dynamic ecological events, could reveal interesting switch points in crabs' relative resource motivation. A fundamental predictor should be which resource (shells or food) is currently most limiting in the population: At sites where hermit crabs have few shells, they should be more attracted to carrion associated with shell cues; whereas at sites where hermit crabs have abundant shells but limited food, they should be attracted to carrion, even if it lacks shell cues.

While hermit crabs aggregated quickly for carrion in our study and while these aggregations persisted across time, the precise behaviors that crabs exhibited within their aggregations could not be quantified under the field conditions of our experiments. We did consistently observe hermit crabs feeding on both forms of carrion (gastropod and mussel) by picking through the mesh and eating bits of torn flesh. However, it was unclear whether crabs might have also exhibited some behaviors related to shell acquisition (e.g., by fighting or 'piggybacking' on each other's shells in anticipation of a shell switch). Such behaviors are possible, because even if crabs are originally attracted to a site for the purpose of eating, other motivations could subsequently surface (Laidre 2010, 2012). Controlled laboratory experiments (e.g., Tricarico et al. 2011) would enable greater focus on crabs' fine-grained behavior within aggregations.

Even if hermit crabs may be motivated to eat carrion, the question remains how their carrion scavenging compares with other scavenging species in the ecosystem (Britton and Morton 1994; King et al. 2007; Breithaupt and Theil 2011). Our study suggests that hermit crabs can be swarms of swift scavengers, performing an essential carrion scavenging role in intertidal ecosystems: Hermit crabs were consistently the fastest to arrive at our sites, accumulated in the largest numbers, and their aggregations persisted across extended time periods. Notably, we even detected an increase in hermit crab numbers in the live mussel condition (when examining the mean number of individuals across the entire test period). This increase, even though the mussel was not even smashed, is probably due to mussels partially opening their shells after being dislodged from their bed, which may result in the release of at least some chemical cues. Hermit crabs' fine chemosensory abilities apparently enable them to locate such sites despite fewer available chemical cues.

Our results show that hermit crabs are dominant scavengers; however, these results do not imply that hermit crabs are necessarily the most dominant scavenger at all times. All our experiments were conducted at low tide, so it is possible that at high tide, other species might outcompete hermit crabs for carrion. Indeed, at high tide, fish and other larger scavengers might be able to arrive at carrion sites faster than hermit crabs. Additionally, hermit crab behavior may differ at high tide because the influx of large predators can force some hermit crab species to take refuge in protective crevices (Bertness 1981). Only by conducting identical experiments at high tide, perhaps using underwater cameras to record the attracted scavengers, could the generality of hermit crabs' scavenging dominance be tested (though see Ramsay et al. 1997 for evidence of scavenging dominance in sub-tidal hermit crabs). It is clear from studies in other areas (e.g., the sandy shores in Hong Kong; Morton and Yuen 2000) that hermit crabs are not always the most dominant scavenger: Other sympatric species, such as carnivorous gastropods, can sometimes outcompete them. Nevertheless, at rocky intertidal sites in California, hermit crabs appear to perform a generalized scavenging role that, at low tide, outstrips any other sympatric species, invertebrate or vertebrate.

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