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Can a scavenger benefit from environmental stress? Role of salinity stress and abundance of preferred food items in controlling population abundance of the snail *Lirabuccinum dirum*

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ABSTRACT

Food availability can be an important determinant of the abundance and distribution of animals. For scavengers, however, food availability is determined not only by the abundance of species used as food but also by the rate at which individuals of these species die and become available to the scavengers. Environmental conditions sufficiently stressful to kill individuals might play a role in providing food for scavengers, but only if scavengers can tolerate harsher conditions than their food species. We examined the roles of species preferences, abundance of food species, and ability to survive reduced salinity in determining the abundance of a scavenger, the intertidal gastropod *Lirabuccinum dirum*. Laboratory experiments confirmed that *L. dirum* is an opportunistic scavenger, consistently preferring dead specimens over stressed or healthy specimens, and also preferring the mussel *Mytilus trossulus* over 5 other species of benthic invertebrates. *L. dirum* was highly tolerant of low salinities, surviving up to 10 d in treatments of only 12.4 PSU salinity (40% of full salinity), and was significantly more tolerant of low salinity conditions than the abundant barnacle *Balanus glandula*. Surveys at 16 field sites in Barkley Sound, on the west coast of Vancouver Island, revealed that *L. dirum* population density was unrelated to densities of individual food species, and only weakly correlated with total density of all food species combined. Total densities of food species were $\geq$123 individuals per m^2 at all sites, which may be sufficient to sustain a population of *L. dirum*, in which case food availability would not be a limiting factor. *L. dirum* population density was strongly related to salinity stress; the species was present at all sites in the 2 highest salinity stress categories and absent from most sites in the 2 lowest salinity stress categories. These findings confirm the hypotheses that *L. dirum* is more tolerant to salinity stress than some of its food species and that *L. dirum* lives primarily in habitats that experience relatively high salinity stress. Periodic mortality of benthic invertebrates due to salinity stress may therefore be an important factor determining food availability to *L. dirum*, and thus its population abundance. *L. dirum* may therefore take advantage of sites with fluctuating salinity, as these sites could provide a periodic supply of dead or stressed specimens.

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1. Introduction

Variations in population abundance over time and space are common in benthic marine invertebrates (Eckert, 2009; Uthicke et al., 2009). Such variations can be strongly associated with variations in food abundance, as is the case in the predatory intertidal snail *Nucella canaliculata* (Connell, 1970; Weiters and Navarrete, 1998) and in the Atlantic rock crabs *Cancer irroratus* and *Cancer borealis* (Ojeda and Dearborn, 1991). Food abundance can also be a major determinant of the distribution and abundance of marine scavengers, such as the giant isopod *Bathynomus giganteus*, or the snail *Nassarius festivus* (Britton and Morton, 1994). In the case of scavengers, however, food availability is determined not only by the abundance of food species but also by the rate at which individuals of these species die and become available to the scavengers.

The scavenging mode of feeding is common in benthic marine invertebrates, having been reported in a number of echinoderm (Brewer and Konar, 2005), polychaete (Lee et al., 2004) and gastropod species (Eden et al., 2003; Morton, 1990; Tan and Phuah, 1999). In most species, the scavenging mode is facultative or opportunistic: the animal prefers carrion, but will also occasionally feed as predators on stressed or healthy animals (Brewer and Konar, 2005; Britton and Morton, 1994; Eden et al., 2003; Morton, 1990). Alternatively, an animal may be primarily a predator, feeding on dead specimens only when live specimens are unavailable. If a species prefers to feed as a predator, then food availability in a given habitat will be largely determined

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by the abundance of their prey. On the other hand, if a species is primarily a scavenger, then food availability will depend not only on the local abundance of animal populations, but also on the occurrence of conditions causing the death of some animals; more specifically, conditions that kill animals without carrying their bodies beyond the reach of the scavenger (e.g. by waves) or removing all the tissues of the dead animal (e.g. consumed by a predator). Conditions that would satisfy the above criteria include periodic extremes of salinity, silt deposition, desiccation stress and temperature. In coastal habitats, the osmotic stress of periodic reductions in salinity can cause mortality in benthic invertebrates (Irlandi et al., 1997).

Conditions that are sufficiently stressful to kill individuals of species used as food, however, might also harm a scavenger; a scavenger would only benefit from the periodic occurrence of stressful conditions if it is able to tolerate harsher conditions than the species it uses as food. There is some evidence that this might be the case; scavengers often do have morphological, physiological, or behavioral adaptations that enhance their tolerance to environmental stress. For example, scavenging snails of the genus *Nassarius* have an efficient osmoregulatory system that allows them to tolerate large fluctuations in salinity and survive at both high and low salinity extremes (Cheung, 1997; Morton, 1990); these snails are able to survive for brief periods in salinities as low as 12 PSU. Other marine scavengers, such as the epibenthic isopod *Orchomene obtusus*, are able to slow their metabolic rate and survive for extended periods in anoxic conditions while scavenging in the benthos, periodically moving up to oxygenated waters to conduct aerobic respiration (De Robertis and Rau, 2001). It is not clear, however, if scavengers might have physiological tolerance limits that exceed those of their food species, or the nature of the relationship between the abundance of scavengers and levels of environmental stress. To resolve these issues, we examined the roles of food species abundance and environmental stress in determining the abundance of a scavenger, the gastropod *Lirabuccinum dirum*.

L. dirum is common in many intertidal and shallow subtidal habitats along the west coast of North America, from northern Alaska to southern California (Lloyd 1971; Louda 1979). This species has nevertheless been the object of few studies to date, and very little is known of its feeding habits or factors influencing its abundance. *L. dirum* is believed to have a generalist diet, feeding on several species of benthic invertebrates (Lloyd, 1971; Louda, 1979). Lloyd (1971) and Louda (1979) each reported that *L. dirum* will scavenge dead animals, but Louda (1979) also reported that *L. dirum* will attack and consume live invertebrates. The species preferences of this species are not well understood, and it remains unclear whether *L. dirum* prefers to feed as a scavenger or whether the scavenging mode of feeding is secondary to a predatory lifestyle. In addition, the relationship between habitat features and the abundance of *L. dirum* is not understood.

In this study, we test 3 hypotheses: (1) *L. dirum* is an opportunistic scavenger that prefers to feed on dead animals, (2) *L. dirum* will have a higher tolerance of stressful conditions than the species it uses as food, and (3) *L. dirum* is most abundant in habitats that are stressful and in which species used as food are abundant. To test these predictions, we experimentally determined: (1) the food item health condition preferred by *L. dirum* (i.e. whether *L. dirum* prefers healthy, stressed or dead specimens); (2) the preferred food species; (3) the tolerance limits of *L. dirum* and of its food species to reduced salinity; and (4) the extent to which the abundance of *L. dirum* in the field can be explained by the combined effects of food abundance and levels of 2 physical parameters of the habitat: salinity stress and wave exposure.

2. Materials and methods

The field sites selected for this study were located in Barkley Sound, on the western side of Vancouver Island, British Columbia, Canada (Fig. 1). All laboratory experiments were carried out at the Bamfield Marine Sciences Centre.

2.1. Feeding preferences: health condition

To test the hypothesis that *L. dirum* is primarily a scavenger, this first set of experiments examined preferences of *L. dirum* for specimens of 3 different health conditions: healthy, stressed, or dead. This test was performed with 6 potential food species: the chiton *Mopalia muscosa*, the limpet *Tectura scutum*, the snails *Littorina sitkana* and *Tegula funebralis*, the mussel *Mytilus trossulus* and the barnacle *Balanus glandula*. These species were selected because they are generally abundant and often co-occur in the intertidal zone with *L. dirum* (personal observations), and based on observations by Lloyd (1971) and Louda (1979) of *L. dirum* feeding on these species.

Twenty *L. dirum* were collected from an intertidal site in Grappler Inlet (site 16, Fig. 1), each placed individually in a screened treatment cage (11 cm × 11 cm × 5 cm) in a tray with flowing seawater, and allowed to acclimatize for 3 d. Twelve hours before starting the experiment, the seawater was drained from the tray to simulate a low tide and stimulate a foraging response when the tray refilled (Louda, 1979). Also, 3 d before starting the experiment, 60 individuals of each potential food species were collected from the field; 20 individuals of each species were placed in a tray with flowing

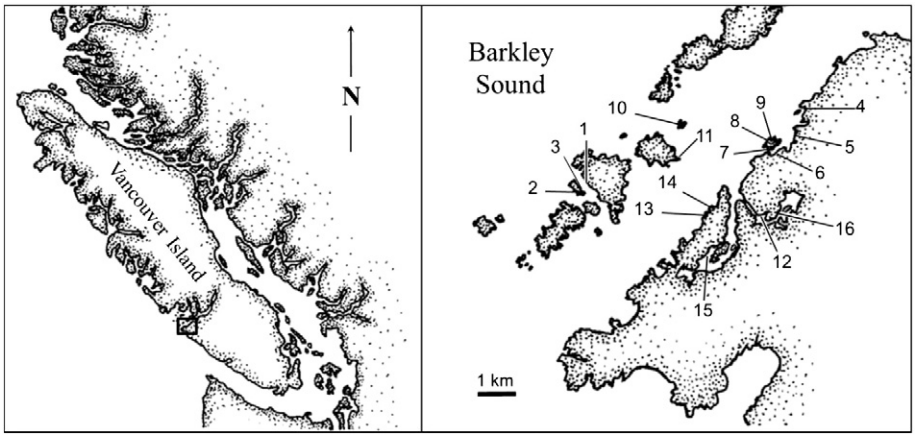

Fig. 1. Locations of the 16 field sites in Barkley Sound, on the west coast of Vancouver Island, British Columbia, Canada. Diana Island (1); exposed side of Seppings Island (2); sheltered side of Seppings Island (3); northeast Roquefeuil Bay (4); central Roquefeuil Bay (5); southwest Roquefeuil Bay (6); southwest tip of Dixon Island (7); western Dixon Island (8); northern tip of Dixon Island (9); Wizard Islet (10); Self Point on Helby Island (11); Port Desire (12); Eagle Point (13); Scott's Bay (14); Burlo Island (15); upper Grappler Inlet (16). Map modified from Gosselin and Chia (1995).

seawater, 20 were euthanized by freezing, and 20 were placed in an incubator without water for 12 h at 30 °C to simulate stressful low tide conditions. Prior to starting the experiment, each specimen was marked with a series of small dots of nail polish as described by Gosselin (1993) to differentiate dead, stressed and healthy individuals, and to allow for rapid identification of specimens during the experiment. Three specimens, one of each health condition, were then simultaneously added to each of the treatment cages. Based on preliminary laboratory trials showing that most *L. dirum* would begin feeding on dead or stressed specimens within minutes or, at the most, a few hours, the cages in the food selection trials were examined every 4 h for 12 h to determine which specimen was attacked first by each *L. dirum*.

The above experiment revealed a strong preference for dead specimens. Consequently, 2 follow-up trials were performed to address the following additional questions: (i) in the absence of dead specimens, does *L. dirum* prefer stressed over healthy specimens? (ii) in the absence of dead or stressed specimens, will *L. dirum* attack healthy specimens? The design of these trials was similar to that of the first trial described above, except for the following modifications: in the second trial, one stressed and one healthy specimen were offered to each *L. dirum*. In the third trial only live specimens were offered to *L. dirum*. Also, the second trial involved only *M. trossulus* and *Tegula funebralis*, as these were found to be the preferred species in a preliminary species selection experiment. The third trial involved *B. glandula* and *Tectura scutum*; these species were used instead of *M. trossulus* and *T. funebralis* because they are abundant in the field and because the second trial had already confirmed that *L. dirum* would not attack stressed or healthy *T. funebralis* and some *L. dirum* did attack healthy *M. trossulus*.

2.2. Feeding preferences: species

In this experiment, several species were simultaneously offered to individual *L. dirum* to determine *L. dirum*'s species preferences. Only euthanized specimens were offered to *L. dirum* in this experiment, based on the strong preference for dead specimens observed in the previous experiment. Two sets of trials were carried out: in the first set of trials, individual *L. dirum* were simultaneously offered one individual of each of the 6 potential food species used earlier in the health condition experiment. This species selection experiment was otherwise carried out in the same way as the experiment on health condition preferences. These trials revealed 3 species (*M. trossulus*, *T. funebralis* and *T. scutum*) to be preferentially consumed by *L. dirum*, and therefore a second set of trials was conducted using only these 3 species to elucidate *L. dirum*'s preference among these species.

2.3. Salinity tolerances

This experiment was carried out to test the hypothesis that *L. dirum* has a greater physiological tolerance to periods of reduced salinity than the species it uses as a food source. We used the preferred species, *M. trossulus*, as well as *B. glandula*, the most abundant and widespread species at our field sites. Individuals of each species were put into 4.5 l containers differing in salinity but all held at 10 °C and aerated with air stones. The water was changed every 2 d with fresh treatment water.

This experiment consisted of 2 trials. In the first, *L. dirum* and the 2 species were exposed to control (100%) seawater and to dilutions of 80%, 60%, 40% and 20% of full seawater, prepared with seawater and distilled water (i.e. salinities of 31.3 PSU, 25 PSU, 18.8 PSU, 12.5 PSU and 6.3 PSU, respectively). All of these treatments, except for the lowest salinity, are in the range of surface salinities reported for Barkley Sound, where salinity levels between 10 and 20 PSU occur during the winter (Rumrill, 1989) and can occur for brief periods at other times of the year after significant storm events (Garza and Robles, 2010). The second trial focused on the lower range of salinities, using seawater dilutions of 55%, 50%, 45%, 40%, 35%, 30% and 25% (i.e. salinities of 17.2 PSU, 15.6 PSU, 14.1 PSU, 12.5 PSU, 10.9 PSU, 9.4 PSU and 7.8 PSU, respectively). Each treatment involved 3 replicate tanks per species, each tank containing 10 individuals of one species. The 2 trials in this experiment each ran for 10 d; each individual was inspected for mortality on day 10 in the first trial, and on days 2 and 10 in the second trial. Dead individuals noticed during the course of the trials were removed from the treatment tanks when found.

2.4. Abundance in the field

This last study examined the relationship between the abundance of *L. dirum*, the abundance of food species, and 2 habitat features. This was accomplished by surveying 16 field sites within the Trevor Channel area of Barkley Sound that varied substantially in exposure to reduced salinity and to wave action. At each site we documented the abundance of *L. dirum* and of potential food species, and also assessed the salinity and wave exposure conditions of the site.

The abundance of *L. dirum* and food species at each site was assessed by a transect survey, in which two 30 m transects were set parallel to the shoreline; one transect was positioned just above the lower edge of the zone colonized by the barnacle *B. glandula* (i.e. approximately 2.5 m above mean lowest low tide) and the second was positioned lower, at 1.5 m above mean lowest low tide. Each transect consisted of ten 50 × 50 cm quadrats spaced at 3 m intervals; the sampling design therefore consisted of 2 transects × 10 quadrats per transect = 20 quadrats per site. In each quadrat, we counted the number of *L. dirum* as well as the number of individuals of all common animal species: all limpet species combined (*Discurria insessa*, *Lottia pelta*, *L. instabilis*, *L. asmi*, *L. digitalis*, *L. ochracea*, *L. painei*, *Tectura persona*, *T. scutum*, and *T. fenestrata*), the chiton *Mopalia muscosa*, the snail *Tegula funebralis*, all littorine snails combined (*Littorina sitkana*, *L. subrotunda*, and *L. scutulata*), the mussel *M. trossulus*, and all barnacle species combined (*B. glandula*, *Semibalanus cariosus*, and *Chthalamus dalli*).

The distribution pattern of *L. dirum* within each site was determined by calculating the Standardized Morisita Index using the Pop Tools software (Hood, 2010). Early in the study it became apparent that the distribution of *L. dirum* was clustered; since this had the potential to affect transect survey results, we decided to also use a second, complementary approach to assess the overall abundance of *L. dirum* at each site. The entire site, from low tide water line to high tide mark, was carefully examined by 2 observers for 15 min, including cracks, crevices and the undersides of rocks and seaweed. Observers recorded their assessment on a 10 point scale ranging from 0 to 9, with 0 indicating the species was absent and 9 indicating the species was extremely abundant. These independent assessments by the 2 observers were then averaged to obtain a single relative abundance index value for the site.

The field sites surveyed in this study were selected by initially consulting marine charts to identify shores likely to vary in terms of degree of shelter from wave action and also varying in proximity of freshwater input (rivers and streams) and potential for mixing of freshwater with saltwater (e.g. confined inlets or wave-exposed shores); these parameters are important determinants of the extent to which local surface salinity varies over time (Thomson, 1981). Each site was then visited by 2 observers to make *in situ* observations before finalizing the selection. The selected sites were then assigned to one of 4 categories of salinity stress based on *in situ* salinity measurements, the proximity and flow rate of rivers and streams, and potential for rapid mixing of freshwater with saltwater by waves or tidal currents; sites assigned to the “lowest salinity stress” category were far from any river or stream and were expected to experience significant vertical mixing due to wave action or tidal currents, whereas sites assigned to the “highest salinity stress” category were in close

proximity to the estuary of a river with significant flow and would experience very limited vertical mixing. Each site was also assigned to one of 4 categories of wave exposure based on direct observations of wave exposure, intertidal species composition and proximity of terrestrial vegetation to the high tide mark, as in Gosselin and Rehak (2007); sites assigned to the "low exposure" category were highly sheltered from wave action and were consistently calm, whereas sites assigned to the "high exposure" category had little protection and experienced most of the impact of incoming ocean waves and surge. All of our field sites were within Barkley Sound; none were on the open coast where full exposure to oceanic waves and surge occurs.

3. Results

3.1. Feeding preferences: health condition

During the 12 h of this first trial 70–100% of the *L. dirum* fed on a food item, indicating that *L. dirum* was not indisposed by the laboratory settings and that it will use any of these species as a food source. The trial also revealed an unambiguous preference for dead specimens; every *L. dirum* that fed on a food item in this trial (99 of the 120 snails) chose the dead specimen rather than the healthy or stressed specimens, regardless of species.

In the second trial, examining *L. dirum*'s preference between healthy and stressed specimens, 16 of the 20 *L. dirum* that were offered *M. trossulus* fed on a food item; no *L. dirum* attacked *T. funebralis*. Of the 16 snails that attacked *M. trossulus*, 13 (81%) attacked the stressed specimens, significantly more than expected if there had been no preference between healthy and stressed specimens (G-test with Yates' correction, Zar, 2010: $G = 5.371$, $n = 16$, $df = 1$, $p = 0.02$).

In the third trial, in which *L. dirum* were only offered healthy *B. glandula* or *Tectura scutum*, no *L. dirum* attacked *B. glandula* and 2 of 20 snails attacked *T. scutum*. These results are consistent with preliminary trials (unpublished data) in which *L. dirum* ignored healthy specimens of various species for up to 10 d even when no other food type was available.

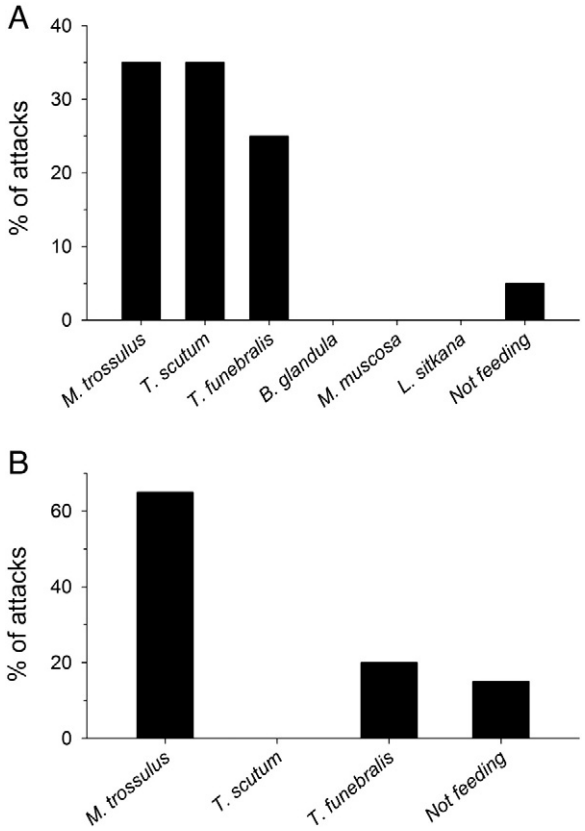

Fig. 2. Proportion of *Lirabuccinum dirum* attacking each species in the species selection experiment, as well as the proportion of *L. dirum* that did not feed. Only dead specimens of each species were offered to *L. dirum* in this experiment, and only the first specimen attacked was recorded. A. Trial in which *L. dirum* were offered one specimen of all 6 species. B. Trial in which *L. dirum* were offered one specimen of the 3 species attacked in the previous trial. In both trials, attack frequencies were significantly different from random (see text).

3.2. Feeding preferences: species

When simultaneously offered dead individuals of all 6 food species, *L. dirum* did not select their first food item randomly ($G = 26.778$, $n = 20$, $df = 5$, $p < 0.001$). In this species preference trial, only 3 of the 6 species were consumed (Fig. 2A): *M. trossulus, T. scutum* and *T. funebralis*. In the second species preference trial, in which only the above 3 species were offered, the number of *L. dirum* consuming each of these species was again significantly different from the numbers expected if *L. dirum* had been selecting their food items randomly ($G = 18.803$, $n = 17$, $df = 2$, $p < 0.001$). Most *L. dirum* chose *M. trossulus* as their first food item (Fig. 2B), revealing *M. trossulus* to be the preferred food source, and *T. funebralis* and *T. scutum* to be secondary preferences.

3.3. Salinity tolerances

The 3 species included in the salinity tolerance experiments all demonstrated an effective tolerance to modest reductions in salinity, but differed in their response to substantial reductions. In the first salinity tolerance trial, *B. glandula* experienced substantial mortality when exposed to water at 60% or less of full seawater, and mortality was 100% for all 3 species in the 20% dilution treatment (Fig. 3A), suggesting the threshold of salinity tolerance for these species to be within the 20–60% range. The second trial, focusing on dilutions of 25–55%, revealed substantial differences among the 3 species in tolerance to salinity. *M. trossulus* was the most tolerant, all individuals surviving in all salinity treatments for the first 2 d and most individuals surviving 10 d in solutions diluted down to 40% of full seawater (Fig. 3B, C). *B. glandula* was the least tolerant of reduced salinity, with mortality occurring in all treatments at ≤50% of full salinity within 2 d. The tolerance of *L. dirum* for salinity stress was intermediate between that of *M. trossulus* and *B. glandula*. *L. dirum* was more sensitive than *M. trossulus* to short-term exposure to solutions of 25–35% of full seawater, but otherwise the 2 species experienced exactly the same mortality levels in other treatments on day 2 and in all treatments on day 10; mortality of these 2 species on day 10 in the 40% dilution treatment were not significantly different (*t*-test: $t = 1.387$, $df = 4$, $n = 6$, $p = 0.238$). *L. dirum* was more tolerant than *B. glandula* to short or long term exposure to dilutions of 35–50% (Fig. 3B, C), although some *L. dirum* did die in the 35 and 40% treatments. Mortality of these 2 species in the 35% treatment were not significantly different on day 2 (*t*-test: $t = 1.357$, $df = 4$, $n = 6$, $p = 0.246$), but were significantly different by day 10 (*t*-test: $t = 3.900$, $df = 4$, $n = 6$, $p = 0.018$).

3.4. Abundance in the field

L. dirum were found in the transect surveys at 5 of the 16 field sites, at densities ranging from 1.4 to 31.6 individuals per m^2. At each of these 5 sites *L. dirum* was distributed in a clustered pattern, as revealed by Standardized Morisita Index values ranging from 0.526 to 0.732; all index values were larger than 0.5 and thus significantly different from a random distribution pattern (Krebs, 1999; Myers, 1978). A linear regression between the average abundance estimates per site obtained from transect surveys and the abundance

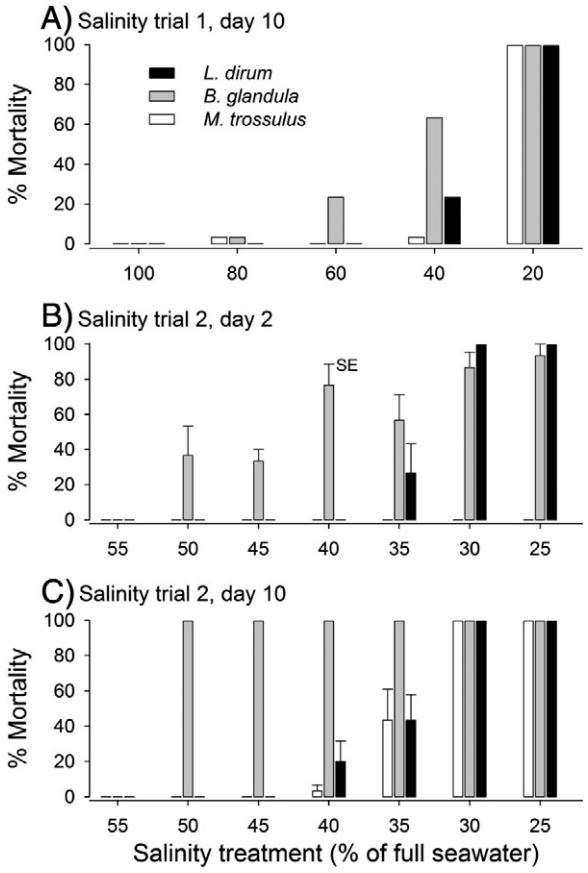

Fig. 3. Mortality of *Lirabuccinum dirum*, *Balanus glandula* and *Mytilus trossulus* when exposed to reduced salinities for up to 10 d. Salinity treatment solutions were obtained by diluting fresh seawater with distilled water.

index values from the timed searches revealed a high degree of coherence between the 2 methods ($R^2 = 0.852$, $F = 80.449$, $df = 15$, $p < 0.001$), suggesting both methods provided effective relative measures of *L. dirum* abundance. There were, nevertheless, a few divergences between the 2 methods, and these occurred mainly at sites with low population abundances; *L. dirum* was found at 5 sites in the transect surveys (sites 1, 5, 6, 15, and 16), whereas the timed explorations revealed *L. dirum* to also be present in small numbers at 3 additional sites (sites 10, 12, and 14). Consequently, data from both abundance estimates were used in each of the following analyses.

Abundance estimates of *L. dirum* for the 16 field sites were not significantly related to the abundances of most animal species at those sites, including the preferred species *M. trossulus* (Table 1). Transect estimates were only significantly correlated with limpet densities, and even this was primarily due to a single site (site 16) with an unusually high density of limpets (934 per m^2) and *L. dirum* (31.6 per m^2), whereas all other sites had limpet densities lower than 380 per m^2. Transect estimates were significantly but weakly related to the total density of all species combined (Table 1, Fig. 4); total combined food species density was not significantly related to timed survey estimates of *L. dirum* abundance. Non-linear relationships were not apparent in scatterplots relating *L. dirum* abundance to individual species.

L. dirum abundance did vary substantially, however, as a function of salinity stress (Fig. 5) and wave exposure (Fig. 6). A non-parametric Spearman rank-order correlation analysis, in which all sites within a salinity stress category were given the same rank, revealed a strong correlation between salinity stress category and *L. dirum* abundance estimates as determined by transect estimates ($r_s = 0.742$, $n = 16$, $p = 0.001$) or timed search estimates ($r_s = 0.721$, $n = 16$, $p = 0.002$), abundance increasing with increasing salinity stress levels. Abundance estimates from transect surveys ($r_s = -0.566$, $n = 16$, $p < 0.022$) and timed surveys ($r_s = -0.551$, $n = 16$, $p = 0.027$) were also significantly correlated with wave exposure levels, although in this case abundance estimates decreased with increasing wave exposure levels. Salinity stress and wave exposure, however, were also significantly correlated ($r_s = -0.860$, $n = 16$, $p < 0.001$).

Table 1
Simple linear correlation (Pearson) between *Lirabuccinum dirum* abundance, as determined by transect and the timed survey methods, and the abundance of live invertebrates at 16 field sites in Barkley Sound. For transect survey data, the average density of *L. dirum* per site was used in these analyses. n = 16 for each correlation.

	L. dirum abundance		*L. dirum* abundance	
	Transect surveys		Timed search surveys	
	r	p	r	p
Chitons	−0.107	0.693	−0.279	0.295
Limpets	0.612	0.012*	0.481	0.059
Tegula funebralis	0.155	0.567	0.062	0.819
Littorina spp.	0.059	0.829	−0.065	0.810
Mytilus trossulus	0.175	0.516	0.227	0.398
Barnacles	0.186	0.490	0.015	0.956
Total abundance of food species	0.497	0.050*	0.353	0.180

4. Discussion

4.1. Feeding preferences

The present study found *L. dirum* to have a strong preference for dead specimens, regardless of species, and to be unwilling or unable to successfully attack most live specimens. This finding is consistent with previous studies proposing a scavenging lifestyle in *L. dirum* (Lloyd, 1971; Louda, 1979) and in other species of the family Buccinidae (Ansell, 2001; Eden et al., 2003; Morton, 1990; Tan and Phuah, 1999). *L. dirum* is an opportunistic scavenger, with the ability to attack and consume stressed specimens, although they do so only if dead specimens are unavailable. *L. dirum* only occasionally attacked healthy specimens of its preferred species, *M. trossulus*, and of the limpet *T. scutum*; they did not attack healthy *B. glandula* or *Tegula funebralis* even when no other food options were available. This is consistent with Thompson's (2002) finding that *Buccinum undatum* was unable to feed on live mussels and instead actively scavenged dead or dying mussels.

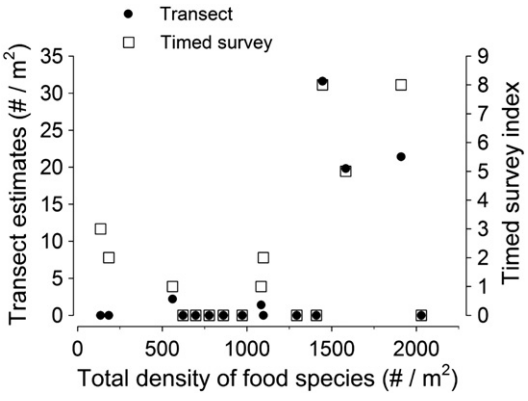

Fig. 4. Relationship between abundance estimates of *Lirabuccinum dirum* and estimates of total food abundance at 16 field sites in Barkley Sound. *L. dirum* abundance was estimated using 2 approaches: transect surveys and timed search surveys. Food abundance was estimated using transect surveys.

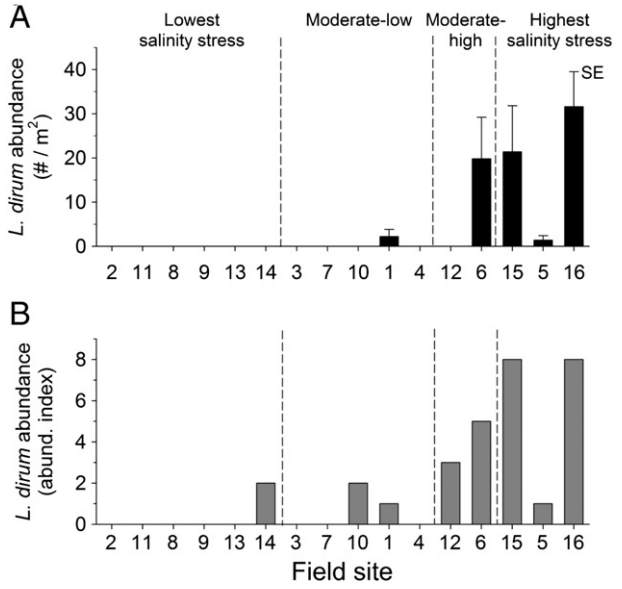

Fig. 5. Abundance of *Lirabuccinum dirum* at each of the 16 field sites grouped according to salinity stress. Abundance was determined by transect surveys (A) and by timed search surveys (B). Dashed vertical lines divide the sites into 4 groups according to salinity stress, from lowest to highest salinity stress.

L. dirum exhibited a strong preference for dead *M. trossulus* as a food source, followed closely by *T. scutum* and *T. funebralis*. When the preferred species were not available, however, *L. dirum* willingly fed on dead specimens of any animal species that was provided, suggesting *L. dirum* may be able to obtain sustenance in any habitat supporting at least modest populations of benthic invertebrates of adequate size, regardless of species. In addition, Ruxton and Houston (2004) proposed that obligate scavengers should have a body mass lower than 1 kg to maintain a positive energy balance and survive. *L. dirum*, with a mass of no more than 50 g including its shell, may therefore feed almost entirely on dead specimens in the field. This may explain observations by Lloyd (1971) and Hoffman (1980) that live specimens of mollusc species used as food by *L. dirum* do not exhibit an escape response until they make contact with the foot or proboscis of *L. dirum*.

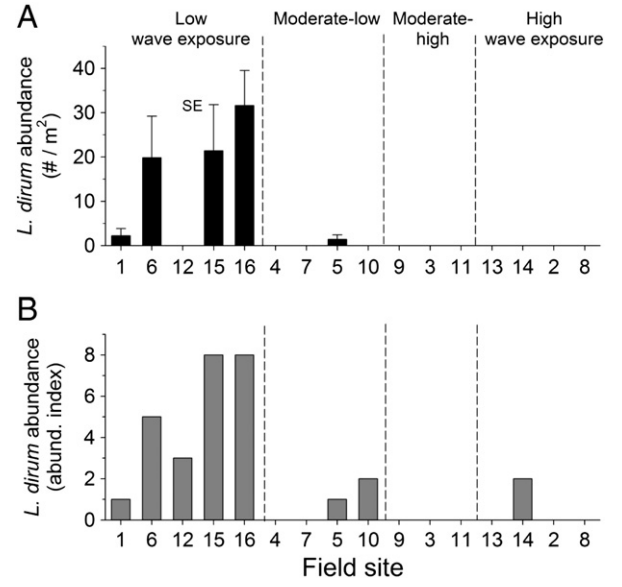

Fig. 6. Abundance of *Lirabuccinum dirum* at each of the 16 field sites grouped according to wave exposure. Abundance was determined by transect surveys (A) and by timed search surveys (B). Dashed vertical lines divide the sites into 4 groups according to exposure to wave action, from low to high exposure.

4.2. Salinity tolerance

L. dirum was quite tolerant to low salinity conditions, being able to survive 10 d in water diluted to 40% of full salinity (i.e. 12.5 PSU). Tolerance of low salinity conditions by *L. dirum* was similar to that of its preferred food species, *M. trossulus*, but was much greater than that of *B. glandula*, one of the most abundant and widespread species on rocky shores in the region. Reductions in salinity to levels below 55% of full seawater (17.2 PSU) for 2 d were sufficient to kill 40% or more of the barnacles. This confirms our second hypothesis that this scavenger is substantially more tolerant to osmotic stress conditions than at least one common food species.

Although *L. dirum* does not have a salinity tolerance advantage over its preferred food source, *M. trossulus*, the salinity tolerance levels of *L. dirum* may nevertheless be sufficient to obtain enhanced access to *M. trossulus* as food. Our feeding experiments revealed that stressed mussels are more vulnerable to *L. dirum* than healthy mussels. Given that *L. dirum* can survive low salinity conditions that are close to the lethal threshold for *M. trossulus*, these conditions would likely cause stress in *M. trossulus* such that salinity stress may indeed make *M. trossulus* more vulnerable to attacks by *L. dirum*. Finally, the ability of *M. trossulus* to cope with elevated levels of osmoregulatory stress was not entirely surprising, as previous studies have demonstrated high osmoregulatory capacity for species in this genus (Braby and Somero, 2006; Qiu et al., 2002).

4.3. Mechanisms controlling the abundance of L. dirum in the field

The field study revealed that the abundance of *L. dirum* at a given site was not determined by the abundance of a particular food species, including that of their preferred species *M. trossulus*, as the density of *L. dirum* was not related to the densities of most individual species. The significant relationship between transect estimates of *L. dirum* density and total density of all food species, however, suggests the overall abundance of species at a site may play a role. This would be consistent with *L. dirum*'s willingness to feed on dead individuals of any species. Nevertheless, the role of food species abundance would at most be modest, as the relationship between transect estimates of *L. dirum* density and total food density was weak, and timed survey estimates were not significantly related to total food density. The lowest total food density observed at our 16 sites was 123.0 individuals per m^2 (site 10), which might be sufficient to sustain a population of *L. dirum*. The abundance of *L. dirum* would then depend more on the occurrence of factors that periodically kill some animals, or at least cause sufficient stress to make them vulnerable to *L. dirum*.

Surveys of our 16 field sites confirmed that *L. dirum* abundance in the field is strongly related to salinity stress; *L. dirum* was present at all 5 sites ranked as moderate–high or highest salinity stress; these sites are in proximity to stream or river estuaries and experience low or moderate wave exposure that would cause limited mixing of the water column. *L. dirum* was absent or at very low densities at sites that were far from estuaries and experiencing substantial mixing of the water column, allowing only minimal fluctuations in salinity. Densities of this species were also strongly correlated with levels of wave exposure, the highest densities being at the most sheltered sites. Salinity stress and wave exposure are correlated, however, making it difficult to tease apart their individual direct influences on population abundance.

Our findings confirm the initial hypotheses that *L. dirum* is more tolerant to salinity stress than at least some of the common species it uses as food and that *L. dirum* lives primarily in habitats that experience substantial salinity stress. Significant freshwater discharge events causing reduced salinity in surface waters of Barkley Sound

and more broadly along the coast of British Columbia are common during the rainy season from October to April (Rumrill, 1989; Scrosati, 2001; Thomson, 1981), and only occasional storm events at other times of the year also cause periods of reduced salinity (Garza and Robles, 2010). However, larval settlement of most benthic invertebrates, including *B. glandula* and *M. trossulus*, occurs during the April to July period (Strathmann, 1987), followed by rapid growth of the recruits. Habitats with frequent osmotic stress during the rainy season can therefore be repopulated by benthic invertebrates during the spring and summer, and during the rest of the year provide a reliable supply of dead or stressed specimens for scavenging species such as *L. dirum*.

All of our study sites were populated by numerous *B. glandula* that are more vulnerable to reduced salinity than *L. dirum*. Mortality of animals due to salinity stress, perhaps combined with other environmental stresses such as silt deposition in habitats with limited water motion (Young and Chia, 1984; Zardi et al., 2008) or desiccation stress and temperature extremes (Gosselin and Chia, 1995; Petes et al., 2008; Schneider, 2008; Schneider and Helmuth, 2007; Trowbridge, 1998), may therefore be the primary mechanism by which *L. dirum* obtains enough food to thrive. An additional mechanism by which salinity stress might influence the abundance of *L. dirum* is by limiting the local abundance of predator species that would kill *L. dirum* or might feed on other benthic species and thus reduce food availability for *L. dirum*. Little is known, however, of the species that feed on *L. dirum*; further work in this regard would be useful as it could help clarify the interactions of biotic and abiotic factors controlling population abundance in *L. dirum*.

Localized sites experiencing short-term fluctuations in salinity on a scale of hours or days are common along coastal regions of the world. Salinity fluctuations at such sites have been shown to cause mortality of a range of benthic invertebrate species, especially species that are sessile or have limited motility, at rates that are higher than at other nearby sites experiencing more stable salinity levels (Irlandi et al., 1997; Rutger and Wing, 2006; Witman and Grange, 1998). The present findings therefore suggest that *L. dirum*, and possibly other benthic scavengers, may take advantage of such localized sites that can provide them with a periodic supply of dead or stressed specimens.

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