Host selection by larvae of a marine insect *Halocladius variabilis*: nutritional dependency or escape from predation?

NORAH E. BROWN, SEAN C. MITCHELL AND DAVID J. GARBARY

Department of Biology, St Francis Xavier University, Antigonish, Nova Scotia, B2G 2W5, Canada

Larvae of the Holarctic marine chironomid, Halocladius variabilis *(Staeger), have strong fidelity to the tuft-forming brown alga,* Elachista fucicola *(Velley) Areschoug, an abundant epiphyte on intertidal fucoids of the North Atlantic. We show that larvae are sufficiently motile to select an algal host in a Petri dish within 3–4 cm, and that larvae show differential behaviour with respect to host selection in the presence or absence of a predator. In the absence of predators 53% of larvae found an algal host within 1 hour; however, after 24 hours, there was no significant difference in host selection. When an isopod predator (*Idotea sp.) was present, more larvae found a host within 1 hour (81%) and* Elachista *was chosen over three of the four other hosts. Furthermore, when larvae were present in* Elachista, *predator (*Carcinus maenus*) success was significantly reduced relative to two other algal hosts. The adaptive significance of* Elachista *as a refuge from predation was confirmed by experiments demonstrating that larval growth with other algal hosts was greater than with* Elachista. *These experiments suggest that microhabitat selection by larvae of* H. variabilis *reveals important tradeoffs for growth and predator avoidance.*

INTRODUCTION

Marine insects, often rare and cryptic, have been largely ignored by marine biologists through exclusion from textbooks and marine biodiversity compilations (e.g. Howson & Picton, 1999; Levinton, 2001; Archambault *et al.*, 2010). The dipteran family Chironomidae, the non-biting midges, provide an exception to the generalization that marine insects are rare with 50 marine species in 17 genera (Hashimoto, 1976; Neumann, 1976). On cold temperate shores of the North Atlantic and Arctic Oceans, the intertidal chironomid, *Halocladius variabilis* (Staeger, 1839), forms a symbiosis with the brown alga *Elachista fucicola* (Velley) Areschoug (hereafter *Elachista*). Larvae of *H. variabilis* can occur in densities of up to 100,000 m^{-2} over a large part of the intertidal zone where *E. fucicola* occurs as an epiphyte on the dominant intertidal fucoids *Ascophyllum nodosum* (Linnaeus) Le Jolis and *Fucus vesiculosus* Linnaeus (Garbary *et al.*, 2005, 2009). This symbiosis is the first to be characterized between a marine insect and seaweed, and Garbary *et al.* (2005) argued that this association was a mutualistic symbiosis. This was based on the apparent fidelity of the larvae and their feeding behaviour. Larvae consume epiphytic diatoms that grow on the assimilatory filaments of their host, and would likely be providing a nutrient contribution to the host, in the form of faecal material, as they move through the basal intertwining host filaments. While larvae have been observed on hosts other than *Elachista* (Garbary *et al.*,

2009; Brown & Garbary, 2010) the egg masses of *H. variabilis* have only been observed on this algal host (Garbary *et al.*, 2005, 2009). Thus, adults of *H. variabilis* are able to select *Elachista* for oviposition while several other potential algal species are not utilized.

The causal basis of host selection during egg mass deposition is unknown. There may be visual and chemical cues from *Elachista* that allow for this selection. Alternatively, adults may be laying eggs in this alga (and others), and the physical structure of *Elachista* may be better at retaining the egg masses against wave action and the returning tide than other hosts. Regardless of the capacity and mechanism for adult host selection, the general abundance and motility of the larvae in *Elachista* suggest that the larval stage has some capacity to select its host. Accordingly, this host fidelity by larvae must represent some benefit with respect to long-term survival and reproduction. Here we describe a series of experiments to determine if larvae can select the species of algal host (*Elachista*), and under what conditions that they might do so. Furthermore, our experiments allow us to distinguish whether host selection by larvae is based on a nutritional benefit to the insect by *Elachista* relative to other algae, or if *Elachista* provided a better refuge from predation than other potential hosts.

MATERIALS AND METHODS

Collection sites and organisms

All algae used in this study (*Elachista fucicola*, *Ceramium virgatum* Roth, *Vertebrata lanosa* (L.) T.A. Christensen, *Pilayella*

Corresponding author:
D.J. Garbary
Email: dgarbary@gmail.com

littoralis (L.) Kjellman and *Cladophora sericea* (Hudson) Kützing) came from Tor Bay (45°10′59″N 61°3601″W) and Drumhead (45°08′44″N 61°36′02″W), in Guysborough County, Nova Scotia. Both sites are fully marine, rocky intertidal sites in which the mid-intertidal zone is dominated by fucoids (mostly *Fucus vesiculosus* and *Ascophyllum nodosum*). The experiments were carried out with various algae, but one alga was always *Elachista*. The other species used were always filamentous (e.g. *Pilayella littoralis* and *Cladophora sericea*) or finely branched (e.g. *Vertebrata lanosa* and *Ceramium virgatum*) (hereafter referred to by generic name) species that were common in the mid to low intertidal zone and were potentially available as hosts at the sites and times of larval collection. All of these, except for *Cladophora*, are common epiphytes of *Ascophyllum*. These algae are the major potential host species for *Halocladius variabilis* larvae based on field observations of abundance *in situ* and presence on *Ascophyllum*. Following collection, algae were kept in a 15°C cold room in seawater for up to four days. Larvae of *H. variabilis* (2–10 mm) were isolated in the laboratory from *Elachista* using forceps to tease apart the host algal thalli. Larvae were measured for Experiment 6 by placing a thin ruler underneath the transparent dish and noting the insects' size to the closest 0.5 mm, using a dissecting microscope. Larvae were maintained in seawater, at 15°C, for a maximum of 48 hours prior to starting experiments. Isopods, *Idotea* (Fabricius, 1798) sp., were collected at the same site; however, green crabs, *Carcinus maenas* (Linnaeus, 1758), were collected in Antigonish Harbour (45°38′37″N 61°56′20″W). Isopods (2–3 cm long) were collected by shaking large handfuls of algae in dishpans or trays partially filled with seaweed and placing the animals into Ziplock bags for transport. Green crabs, with maximum carapace diameter of 3.0 cm, were collected using a minnow trap baited with canned sardines. Isopods and green crabs were maintained in separate dishpans at 15°C until used, typically within 72 hours.

Experiments

Preliminary experiments were conducted to determine if movement of *H. variabilis* differed in the light or dark, the length of time required for larvae to select a host, and the time required for various predation experiments. These experiments (not reported) provided details for protocols of the experiments outlined below. All experiments were carried out at 15°C and a light intensity of 10–15 μmol photons m^{-2} sec^{-1} provided by cool-white fluorescent lamps. Experiments with *H. variabilis* and algae were carried out in plastic Petri dishes 100 × 30 mm; experiments that included predators were carried out in Pyrex deep dishes in approximately 300 ml of seawater. Algal clumps (∼1 cm diameter) for use in experiments were selected haphazardly from the healthiest material. Experiments used variable numbers of replicates, and space constraints meant that data from successive trials were combined for analysis. Experiments outlined below may be considered in three groups that address the different primary questions of this study: (a) do larvae exhibit host preference in the absence of a predator (Experiments 1–2)?; (b) do larvae exhibit different patterns of host selection in the presence of a predator (Experiments 3–5)?; and (c) is host selection based on a nutritional benefit from *Elachista* relative to other algae (Experiment 6)?

Host preference in absence of predators

Do larvae of *H. variabilis* have sufficient motility and behaviour response to select a host, or is the host identity based on vagaries of movement and accidental dislodgement and reattachment? We addressed this issue in two different ways: (a) by addressing the extent to which *H. variabilis* larvae can select their host; and (b) by determining if the larvae will switch hosts once a host is chosen or provided.

EXPERIMENT 1

We hypothesized that *H. variabilis* can select its host, *Elachista*, over other algae in the absence of predators. Three clumps of different algal species were placed 2–3 cm from the centre of the dish in 65 ml of seawater. A single, medium sized (3–4 mm), *H. variabilis* larva was placed in the centre, with a random orientation. After 24 hours the location of the larva was noted (N = 30).

EXPERIMENT 2

We hypothesized that once placed in an algal host, larvae of *H. variabilis* will not move to another host. A single larva was placed in a clump of one of *Elachista*, *Ceramium* and *Vertebrata* and 18 hours later it was determined if the larva had moved to another host 3–4 cm away, or had remained in the same host (N = 30, 10 for each algal host). This experiment controlled for the possibility that larvae may initially find themselves in one host and then migrate to another.

Host preference in presence of predators

Introducing predators into our experimental system allowed us to evaluate if larvae behave differently in the presence of predators, and if the various algal species provide differential refuges from predation. In a preliminary experiment, we established that the two predators (*Idotea* sp. and *Carcinus maenas*) would consume all of the larvae of *H. variabilis* when a single larva was placed in a dish in the presence of a starved individual of the predator (N = 5). The shortest observed consumption times were 20 seconds (green crab) and 1 hour (isopod).

EXPERIMENT 3

We hypothesized that larvae of *H. variabilis* can select their host, *Elachista*, over other algae in the presence of isopod predators. In this experiment, we also considered groups of algal hosts based on morphological similarities. Individual clumps of three algal hosts were placed equidistant from the centre of a Pyrex dish and a single, medium sized *H. variabilis* larva and a single isopod were placed in the centre of each dish (N = 40). After 18 hours, the location of *H. variabilis* larvae was noted. Missing larvae were assumed to be eaten. This experiment attempted to determine host response to the presence of a predator, modifying Experiment 1 by the addition of a predator to the dish.

EXPERIMENT 4

We hypothesized that having chosen a host, larvae of *H. variabilis* will move to *Elachista* in the presence of a predator. A single larva was placed in the centre of a dish with an isopod predator and a choice of three species of algae (*Elachista*, *Vertebrata* and *Pilayella*) (N = 27). After 1 hour the alga chosen by the larva was noted. After 20 hours it was noted

if the larva had moved from that host to another, or had remained in the same host.

EXPERIMENT 5

We hypothesized that survival of *H. variabilis* larvae in the presence of green crabs would be greater when larvae have *Elachista* as a seaweed refuge than any other algal host, i.e. does *Elachista* provide a better refuge from predation than other algal species? Clumps of algae (*Elachista*, *Vertebrata* or *Pilayella*) were placed in the centre of Pyrex dishes and as a control, one dish contained seawater only with no algal refuge. An individual *H. variabilis* larva was placed in each clump of algae and was allowed time to attach to the alga before the predator was introduced (N = 18, for each algal host). A single green crab (carapace width 1–3 cm) was placed in each dish. After 1 hour and 20 hours, the presence and location of the *H. variabilis* larva was noted.

Nutritional benefit

We hypothesized that larvae of *H. variabilis* occur primarily in *Elachista* because of a nutritional benefit from this host.

EXPERIMENT 6

We hypothesized that *H. variabilis* larvae have a higher growth rate in *Elachista* than in other algal hosts. This experiment determined if growth rate of the larvae was a function of food availability or food quality of the host. Clumps of each algal species, 1 cm in diameter (*Elachista*, *Vertebrata* and *Pilayella*), were placed in conspecific pairs in Petri dishes floating in 1 cm of seawater (N = 5 dishes, 2 samples per dish) and five control dishes contained seawater without algae. A single, 2 mm *H. variabilis* larva was placed in each clump of algae. Larval size in each dish was followed over 21 days, and larval length was determined on day 5, 7, 9, 11, 15, 17 and 21. These data were used to create a growth curve. This experiment was carried out twice, giving the same result and we only present data from one of the trials. However, when we considered size at pupation and number of emerging adults, we combined both trials.

Statistical analysis

Experiments 1, 3, and 5 provided frequency data that were analysed using a Chi-square test. If host selection was random, one-third of all *H. variabilis* larvae would be found in each of *Elachista*, *Pilayella* and *Vertebrata*. Therefore the observed results were compared against the 1:1:1 ratio (df = 2). In Experiment 3, we also tested frequency of use considering *Elachista* and *Pilayella* as a group based on their morphological and evolutionary similarities and difference from *Vertebrata*, i.e. they are both brown algae of equivalent sizes and flaccid textures whereas *Vertebrata* is a red alga with a wiry texture. If host selection was by chance, it was also expected that only half of the insects would detect and choose a host. Therefore these observed results were pooled and compared against the 1:1 ratio (df = 1), with no significant difference indicating host detection was random.

For frequency data that had an expected value of less than five (Experiments 2 and 4), Fisher's exact test was used (Zar, 1998). This is similar to the Chi-square test but avoids the limitation of Chi-square when expected values are low. In these analyses, the test was to determine if the ratios in

Experiments 2 and 4 were significantly different from unity, and also from each other.

The mean total growth in Experiment 6 was analysed using an analysis of variance (ANOVA, N = 10). The growth over 21 days was compared among different algae. The Kolmogorov–Smirnov test showed that the data were not normal, and Levene's test gave homogeneity of variance. Given the non-normality, we used the Kruskal–Wallis ANOVA in SPSS (Chicago, Illinois), followed by the *post hoc* Tukey honestly significant difference (HSD) test for multiple comparisons to determine significance of differences in larval growth among algal hosts. We compared the frequency of *H. variabilis* larvae from Experiment 6 living in different algal hosts (*Elachista*, *Vertebrata* or *Pilayella*) to reach pupation size using a Chi-square test. The expected outcome was that larvae would have the same frequency of reaching pupation size regardless of algal host.

RESULTS

Larval behaviour in the absence of a predator

In Experiment 1, *Halocladius variabilis* larvae chose an algal host significantly more often than no host ($P \leq 0.001$) but the larvae chose all algal hosts (*Elachista*, *Vertebrata* and *Pilayella*) with similar frequency ($P = 0.89$) (Figure 1). When a larva did not choose a host, it was often found in the centre of the dish. The experiment was repeated with *Cladophora*, *Ceramium* and *Elachista*, yielding similar results: there was a significant difference in the frequency that an algal host was chosen over no host ($P \leq 0.001$), but there was no difference in the frequency of chosen algal host ($P = 0.64$) (Figure 2). In the absence of predators, 53% of larvae chose a host within 1 hour (N = 30).

In Experiment 2, once placed in a host, 90% of the larvae remained in that host after 18 hours. This complies with our null hypothesis that larvae would not move between hosts ($P = 0.11$, N = 30). These results indicate that once an *H. variabilis* larva is placed in a host, or has chosen a host, in the absence of predators, the larva is unlikely to move. No insects moved from *Elachista*. Of the three hosts that the insects moved to, all algae were chosen equally.
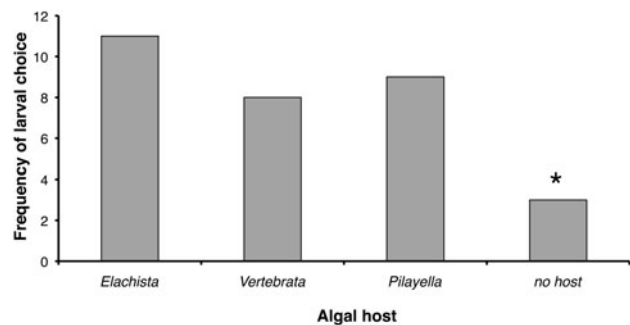

Fig. 1. The frequency of *Halocladius variabilis* larvae choosing an algal host after 24 hours among *Elachista*, *Vertebrata* and *Pilayella* (N = 30). Asterisk above 'No host' indicates larvae chose any algal host significantly more than no host ($P \leq 0.01$).
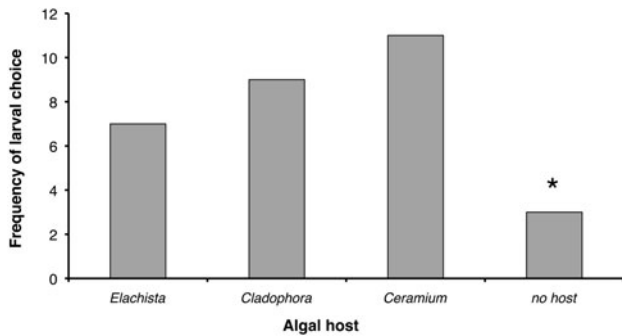
Fig. 2. The frequency of *Halocladius variabilis* larvae choosing an algal host after 24 hours among *Elachista*, *Cladophora* and *Ceramium* (N = 30). Asterisk above 'No host' indicates larvae chose any algal host significantly more than no host ($P \leq 0.01$).

Larval behaviour in the presence of a predator

In Experiment 3, the success rate of the isopod to find the larva was 50% across all algal treatments (N = 40). When predators were present, *Halocladius variabilis* larval behaviour changed in that *Elachista* was chosen significantly more frequently as a refuge than *Cladophora* or *Ceramium* ($P = 0.001$) by the surviving larvae. An algal refuge was chosen significantly more often than no host ($P = 0.0001$) (Figure 3).

When the experiment was repeated with *Elachista*, *Pilayella* and *Vertebrata*, the success rate of the isopod predator was lower, 39% (N = 36). *Elachista* and *Pilayella* were chosen by the surviving larvae with a similar frequency, while *Vertebrata* was not chosen as often as the other two algal hosts. This pattern is not a significant deviation from the 1:1:1 ratio but is a deviation from the 1:2:2 ratio ($P = 0.0003$), which may be important since *Elachista* and *Pilayella* are morphologically similar (Figure 4). In the presence of an isopod predator, 81% of larvae had chosen a host within 1 hour (N = 48). This is significantly more than the 53% when no predator was present as described in Experiment 1 ($P = 0.016$).

In the fourth experiment, once the larvae had chosen a host in the presence of an isopod predator, 19 (i.e. 70.3%) of the larvae stayed in that host for 18 hours, and 8 moved (i.e. 29.6%). This ratio is significantly different from the 27:0 ratio (Fisher's exact test, $P = 0.002$), expected if all 27 larvae did not switch hosts. More larvae switched hosts when there was a predator present (29.6%) than in the absence of a predator (10%) (N = 27, Experiment 4; N = 30, Experiment 2;
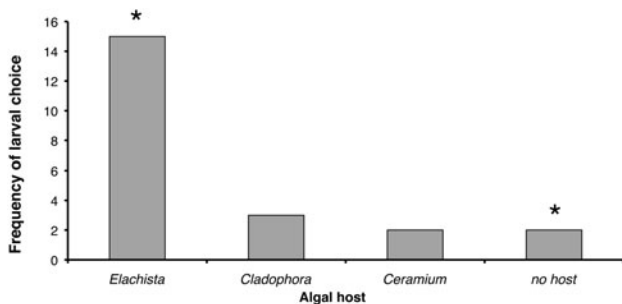

Fig. 4. The frequency of *Halocladius variabilis* choosing an algal host among *Elachista*, *Vertebrata* and *Pilayella* after 18 hours in the presence of an isopod predator (N = 40). Asterisk above *Elachista* indicates significant difference in number between combined *Elachista* and *Pilayella* and *Vertebrata* (due to the morphological similarity between *Elachista* and *Pilayella*). The asterisk above 'No host' indicates larvae chose any algal host significantly more than no host ($P \leq 0.01$).

$P = 0.049$). Of the larvae that switched hosts, only one moved from *Elachista*. Of the eight larvae that moved to a new host, the new host was *Elachista* in five trials and *Pilayella* in three trials.

The green crab had a 43% predation success rate across all algal treatments (Experiment 5). The green crabs ate significantly fewer insects that used *Elachista* as a refuge compared with *Vertebrata* and *Pilayella* ($P = 0.032$) (Figure 5).

Nutrional benefit

All larvae in all algal hosts grew over the 21 days experiment (Figure 6) (Experiment 6). The maximum length reached by a larva was 5.5 mm. There were significant differences in growth among the different treatments during the experiment after 21 days (ANOVA, F = 22.267, $P \leq 0.001$). Larvae in all algal treatments grew significantly more than those in the control treatment (*post hoc* Tukey HSD, $P \leq 0.05$, after 21 days) and some insects in the control shrank. Larvae in *Elachista* were smaller than those in *Pilayella* after 21 days (*post hoc* Tukey HSD, $P \leq 0.05$).

In addition, there were differences in the number of insects to reach 5 mm (the minimal pupation size observed in two independent runs of the experiment) among different algal hosts: *Pilayella* 13, *Vertebrata* 9 and *Elachista* 3. Over two

Fig. 3. The frequency of *Halocladius variabilis* choosing an algal host among *Elachista*, *Cladophora* and *Ceramium* after 18 hours in the presence of an isopod predator (N = 40). Asterisk above *Elachista* indicates use of *Elachista* is greater than use of other algae and asterisk above 'No host' indicates larvae chose any algal host significantly more than no host (both $P \leq 0.01$).
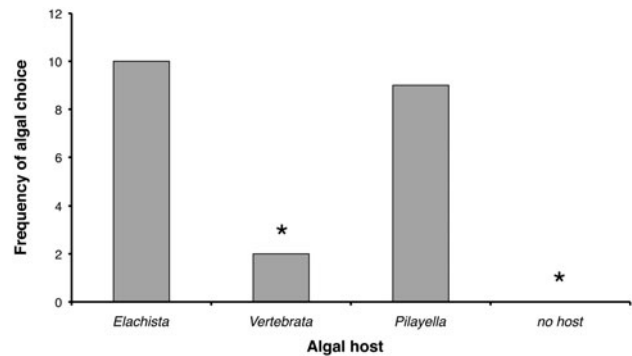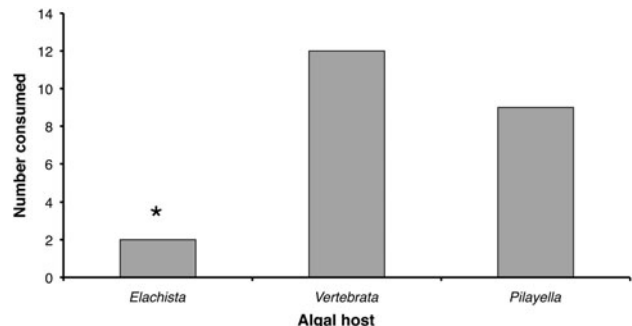

Fig. 5. The number (frequency) of *Halocladius variabilis* larvae eaten by green crabs after 20 hours when *H. variabilis* was using *Elachista*, *Vertebrata* or *Pilayella* as a seaweed refuge (N = 18). Asterisk indicates significantly fewer larvae were eaten out of *Elachista* than any other algae ($P \leq 0.05$).
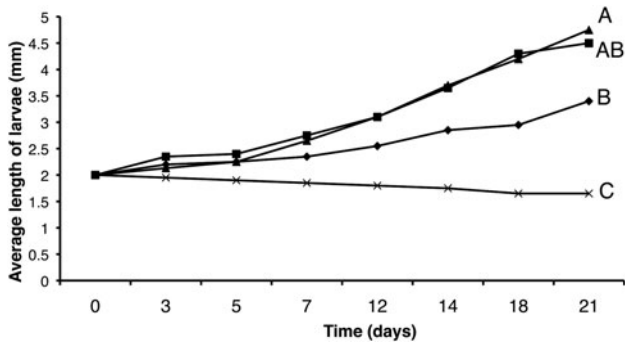
Fig. 6. Growth of *Halocladius variabilis* larvae in different algal hosts: *Elachista* (diamond), *Vertebrata* (circle), *Pilayella* (triangle) and control (square). Error bars represent standard deviation (N = 10). Error bars in control are too small to show clearly; A, B, and C represent significantly different lengths at day 21 ($P \leq 0.05$).
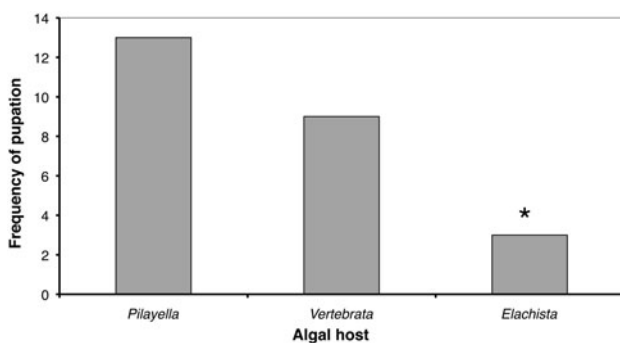

Fig. 7. The number (frequency) of *Halocladius variabilis* larvae living in different algal hosts (*Elachista*, *Vertebrata* or *Pilayella*) to reach 5 mm, common pupation size, after 21 days (N = 20 each). Asterisk indicates significantly fewer larvae living in *Elachista* reached minimum observed pupation size than in other hosts.

trials, 3–4 times fewer larvae reached pupation size (commonly 5 mm) on *Elachista* than on *Pilayella* or *Vertebrata* (N = 20, $P = 0.048$) (Figure 7).

DISCUSSION

In situ, at least three of the epiphytic algae (i.e. *Elachista*, *Pilayella* and *Vertebrata*) are sufficiently abundant that thalli on individual or different host fronds of *Ascophyllum* would be close enough (i.e. from overlapping to centimetres apart) for larval migration, particularly at low tide. While less abundant, the epiphytic or epilithic fronds of *Cladophora* or *Ceramium* also would be often within range of larval motility. Our laboratory experiments clearly demonstrate that larvae of *Halocladius variabilis* have sufficient motility and behavioural capacity to select their host. Larvae will preferentially select *Elachista* (and to a lesser extent *Pilayella*) as that host, in the presence of potential predators. This is consistent with previous field observations (Garbary *et al.*, 2005, 2009; Brown & Garbary, 2010; Garbary & Brown, in press). In addition, the presence of a predator prompted more larvae to switch algal hosts, from a lesser quality refuge to a better quality refuge, which for the majority of those insects was *Elachista*, although some switched to morphologically similar *Pilayella*. Importantly, fewer *H. variabilis* larvae were

eaten by green crabs when taking refuge in *Elachista* than in any other host. Hence, this experiment demonstrates that *Elachista* provides the best refuge from predation of those offered for *H. variabilis*, and is therefore preferred by *H. variabilis* larvae when predators are present. We have further demonstrated that the host selection of *E. fucicola* is based on a refuge from predation, and not by its host providing a greater nutritional benefit for growth than other potential algal hosts. This is the first time that such associations have been demonstrated for a marine insect, and is a key demonstration of the tradeoffs that organisms face when selecting habitat for food supply and protection from predation. This pattern has been demonstrated for other marine invertebrates, including gastropods, annelids and crustaceans (e.g. Hay *et al.* 1990; Holmlund *et al.*, 1990; Duffy & Hay, 1991), and most recently for amphipods (Lasley-Rasher *et al.*, 2011). Our explanation for these results is the fact that individual thalli of *Elachista* are longer lived (i.e. up to one year) whereas thalli of *Pilayella* are much more ephemeral (Garbary, 1976). Consequently, *Elachista* provides a more stable habitat that has duration over the entire larval stage of the insect which likely has a maximum longevity of six months to one year (Garbary *et al.*, 2009).

When we began this study we recognized the possibility that apparent host fidelity of larvae to *Elachista* may be explained simply as a consequence of adult *H. variabilis* ovipositing egg masses in this host. *Elachista* is the only host where egg masses have been found (Garbary *et al.*, 2009; Tarakhovskaya & Garbary, 2009; Brown & Garbary, 2010) and additional experiments would clarify the adaptive basis of this association. Namely, is the association based on the abundance of *Elachista* at appropriate tidal elevations, or does this host provide security for those egg masses (i.e. lower predation and lower risk of physical removal by wave action)? Regardless, the visual or chemical cues by which the adults select *Elachista* warrant further study.

The association of *H. variabilis* with *Elachista* in Nova Scotia is part of a larger community, including: (1) the primary host of *Elachista*, *Ascophyllum nodosum*; (2) its obligate endophytic fungus, *Mycophycias ascophylli* (Cotton) Kohlmeyer & Volkmann-Kohlmeyer; and (3) its host-specific, epiphytic red alga, *Vertebrata lanosa*. This set of interacting species forms a complex symbiotic community (Garbary *et al.*, 1991; Garbary & MacDonald, 1995; Garbary & Deckert, 2001; Xu *et al.*, 2008; Toxopeus *et al.*, 2011). While we have not established any interactions between *H. variabilis* and the other members of the community, we suggest here some possible interactions. Given the motility of *H. variabilis*, larvae may be able to access the pit formed at the point of colonization of *Elachista* on *A. nodosum* described by Deckert & Garbary (2005). This location, the interior of damaged air bladders, or other surface wounds on *A. nodosum* (described by Longtin & Scrosati, 2009) could potentially provide effective refuge from predators. If *H. variabilis* can access these chambers, it would provide even greater refuge from potential predators than the upper portions of its host thallus. Reciprocally, *H. variabilis* larvae could potentially provide nitrogenous faecal material to *A. nodosum* (Garbary *et al.*, 2005). Therefore, it may be important that *H. variabilis* selects an epiphyte on *A. nodosum*, which provides a choice of refuges, and not any other potential algal host.

The experiments described here dealt only with invertebrate predators, and it is possible that fish predation is also

important. While a preliminary experiment using Atlantic silversides (*Menidia menidia* (Linnaeus, 1766)) was unable to demonstrate selective predation by fish on larvae in different algal hosts (N. Brown, unpublished observations), fish predation on chironomids is important (e.g. Collins, 1982; Williams & Williams, 1998; James-Pirri *et al.*, 2001; Alford & Beckett, 2007). We did observe head capsules and other fragments of chironomids in faecal material of fish caught in an estuarine site where *H. variabilis* was also present, though the observed head capsules may not have been *H. variabilis*. Extending our experiments to fish predation may provide important insights into predation and food web dynamics of the rocky intertidal zone (Brawley, 1992), especially considering the high production of *H. variabilis* (Garbary *et al.*, 2009). Perhaps because of their cryptic habit, insect larvae are seldom included in the food web structure of the rocky intertidal zone (e.g. Levinton, 2001; Golley *et al.*, 2010). Robles & Cubit (1981) noted that many ecologists have been unaware that Diptera even live in the rocky intertidal zone, and even today, insects are usually omitted from marine invertebrate inventories (e.g. Howson & Picton, 1999).

Although this set of behaviours is unique to a marine insect, similar behaviours have been noted in a caterpillar predator–prey system. The twig-like caterpillar *Selenia dentaria* (Fabricius, 1775) changed its host-selection behaviour based on whether or not a predator was present. In this system, the masquerading caterpillars chose refuges with a high density of twigs when avian predators were about; however, when the predators were absent at night, the caterpillars foraged in more open areas (Skelhorn *et al.*, 2011).

Analogous experiments have been conducted in freshwater with a mosquito *Anopheles pseudopunctipennis* (Theobald, 1901), which inhabits freshwater streams in the tropical Americas (Bond *et al.*, 2005). This system has been well studied due to the medical implications of the malaria-carrying mosquitoes. These mosquitoes lay their eggs exclusively in freshwater algae, primarily *Spirogyra majuscula* Kützing, as this alga is an important part of larval diet, and can support larvae to full development (Bond *et al.*, 2005). As in the *H. variabilis* system, algae are an essential part of the life cycle of these insects. In addition, Bond *et al.* (2005) describe fish as the primary predators for *A. pseudopunctipennis* larvae, and freshwater algae effectively provide refuge for developing larvae from fish. It is clear from other experiments that visual, physical, and chemical cues (both from algae and predators) aid ovipositing adult mosquitoes in selecting appropriate microhabitat for egg laying (Orr & Resh, 1992; Bond *et al.*, 2005; Silberbush *et al.*, 2010) and the presence of certain insectivorous fish reduces oviposition by adult mosquitoes (e.g. Etam & Blaustein, 2004; Louca *et al.*, 2009). Experiments by Orr & Resh (1992) include active *Anopheles* larval selection of high density aquatic macrophytes as a refuge from predation. Late instar *Anopheles* larvae moved directly to vegetation cover and remained there, where they experienced higher survival in high density patches (Orr & Resh, 1992). This is similar to *H. variabilis* larval response to, and survival in, the algal hosts in our experiments.

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Correspondence should be addressed to:
D.J. Garbary
Department of Biology
St Francis Xavier University
Antigonish, Nova Scotia, B2G 2W5, Canada
email: dgarbary@gmail.com