

Ascophyllum (Phaeophyceae) and its symbionts.
IX. A novel symbiosis between *Halocladius variabilis*
(Chironomidae, Insecta) and *Elachista fucicola* (Elachistaceae,
Phaeophyceae) from marine rocky shores of Nova Scotia

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Abstract

Larvae of the marine insect *Halocladius variabilis* (Diptera, Chironomidae) are symbiotic with the filamentous and syntagmatic brown alga, *Elachista fucicola* (Chordariales, Elachistaceae), which, in turn, is epiphytic on the intertidal brown alga *Ascophyllum nodosum* (Fuciales, Fucaceae). On the Atlantic coast of Nova Scotia, *H. variabilis* was found only on thalli of *E. fucicola* with 1–7 larvae commonly present per host thallus. From June to November over 80% of host thalli were colonized. The symbiosis between *E. fucicola* and *H. variabilis* is at least commensal and possibly mutualistic. Evidence for mutualism is circumstantial and based on the host specificity of *H. variabilis* in Nova Scotia, the larger size of hosting versus non-hosting thalli of *E. fucicola* (10 mg vs. 5 mg dry weight, significant at $p < 0.05$), and a significant, positive correlation ($r = 0.44$) between larval number and host dry weight. *E. fucicola* may benefit from grazing by the larvae on the epiphytic diatoms on its assimilatory filaments, and through fecal nitrogen enrichment. This is the first account of a potential mutualistic symbiosis between a marine insect and a marine alga.

Keywords: *Ascophyllum*, *Elachista*, *Halocladius*, diatoms, marine insects, rocky intertidal zone

1. Introduction

Insects typically are considered unimportant components of marine communities and, relative to terrestrial communities, there are few insects in the sea (Williams, 1999). There is little or no mention of insects in recent textbooks of marine botany or marine biology, or they are regarded as terrestrial animals that visit these marine communities (Little and Kitching, 1996; Dawes, 1998; Levinton, 2001; Nybakken, 2001). In contrast, marine insects in entomology texts are considered important components of some marine communities (e.g. Gullan and Cranston, 2004). More specifically, insects can be abundant and diverse in salt marsh and estuarine communities (LaSalle and Bishop, 1987; Williams and Williams, 1998; Giberson et al., 2001).

This is especially the case in warm temperate and tropical estuarine conditions, including salt marshes and mangroves, where chironomids are important ecological components (LaSalle and Bishop, 1987; Goldfinch and Carman, 2000). Even on rocky temperate shores, chironomid larvae may be important as grazers (Robles and Cubit, 1981). Larval stages of Chironomidae have been described as being associated with marine plants and algae (Hashimoto, 1976; Neumann, 1976); however, the nature of the interaction and the specificity of the symbioses have not been investigated.

As part of observations on the fungal and algal symbionts of *Ascophyllum nodosum* (L.) Le Jolis (Garbary and Deckert, 2001), an insect larva was noted as a common inhabitant of the brown alga *Elachista fucicola* (Velley). Areschoug. *E. fucicola* is an obligate epiphyte largely restricted to the intertidal brown algae *Fucus vesiculosus* L. and *Ascophyllum nodosum*. The latter species is the dominant intertidal species on cold temperate shores of the North Atlantic Ocean (Baardseth, 1970). The insect was later identified as the dipteran chironomid, *Halocladius*

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variabilis (Staiger). This species is widely distributed in the Holarctic and is reported from both rocky intertidal and salt marsh habitats (Hirvenoja, 1973; Colbo, 1996; Giberson et al., 2001). Here we describe a novel symbiosis between *E. fucicola* and *H. variabilis* that is at least commensal, if not mutualistic.

2. Materials and Methods

Twice monthly collecting trips were made to Drum Head, Guysborough Co., Nova Scotia (N45°08'44", W61°36'02") from May to December 2001, with monthly collections between December 2001 and January 2002. To establish host specificity, macroscopic intertidal seaweeds were collected from Tor Bay and Drum Head in Guysborough Co. during May–June and returned to the laboratory for microscopic inspection. On each visit, up to 60 fronds of *A. nodosum* (hereafter *Ascophyllum*) were collected. In the laboratory, 50–100 individual thalli of *E. fucicola* (hereafter *Elachista*) were removed from *Ascophyllum* and dissected using fine forceps and a stereomicroscope. The number of larvae of *H. variabilis* (hereafter *Halocladius*) present in each host thallus was recorded. In addition, the occurrence of egg masses and pupal stages was noted. Additional collections of seaweeds were made in southern Newfoundland, and at various sites on the Atlantic coast and the Bay of Fundy to determine the distribution of *Halocladius* and the diversity of its algal associates (Table 1). Latitude and longitude at all collection sites were determined using a global positioning system (GPS) unit (Garmin GPS 12, Olathe, Kansas) with values rounded to the nearest second (Table 1).

Collections of whole thalli of *Ascophyllum* with their epiphytic *Elachista* were refrigerated at 4°C until *Elachista* was removed and then examined with a stereomicroscope or used in experiments. To examine the nature of the interaction between *Elachista* and *Halocladius*, thalli of the former were selected randomly from collections during July–August. Each thallus was dissected and the larvae present were removed and counted. The *Elachista* thalli were then air dried for 24 h on a Kimwipe and then weighed to the nearest 0.0001 g. The dry weight of thalli with and without larvae was compared, and larval number was correlated with host dry weight. Alternatively, whole fronds of *Ascophyllum* were attached basally to a weighted plastic rack placed in large seawater aquarium (at 15°C and ambient summer photoperiod) so that fronds had a vertical orientation. Fronds were desiccated for two hours per day by removing the racks from the water and individual larvae were observed through the open top of the aquarium.

Scanning electron microscopy was carried out by fixing larvae in a solution of 2.5% glutaraldehyde, 0.1 M sodium cacodylate in Millipore-filtered seawater (MFSW) (pH 7.4) for 1 h at 4°C. Larvae were washed in a buffer (pH 7.4) of 0.2 M sodium cacodylate and post fixed in 1.25% osmium

Table 1. Collection sites for *Halocladius variabilis* associated with *Ascophyllum nodosum* in Nova Scotia and Newfoundland, Canada. All sites visited once between May 2 and August 9, 2001, except Drum Head where collections continued until December. Note: sites with minus (–) have *Elachista*, unless stated otherwise.

Site	Presence of <i>Halocladius</i>	Location
Nova Scotia		
Drum Head	+	N45°08'44", W61°36'02"
Captain's Pond	–	N45°40'51", W61°52'08"
Caribou Harbour	–	N45°44'08", W62°39'29"
Tor Bay	+	N45°10'59", W61°21'17"
Chebogue Point	+	N43°44'15", W66°07'04"
Queensport	–	N45°20'53", W61°21'11"
Hampton (Bay of Fundy)	–	N44°54'24", W65°21'04"
The Hawk, Cape Sable I.	+	N43°25'00", W65°36'47"
Harbourville (Bay of Fundy)	–	N45°09'09", W64°48'41"
Lockeport	–	N43°41'46", W65°06'49"
Mahone Bay	–	N44°26'59", W64°22'44"
(No <i>Elachista</i>)		
Meteghan (Bay of Fundy)	–	N44°11'35", W66°10'03"
Northwest Harbour	+	N43°33'56", W65°24'55"
Peggy's Cove	–	N44°29'53", W63°54'09"
(No <i>Elachista</i>)		
Port Maitland (Bay of Fundy)	–	N43°59'11", W66°09'28"
Sandy Cove (Bay of Fundy)	–	N44°29'20", W66°05'26"
St. Margaret's Bay	–	N44°39'50", W63°55'47"
Western Head	+	N43°59'32", W64°39'45"
Lower Whitehead	–	N45°13'05", W61°10'45"
Newfoundland		
Brunette Island	+	N47°16'00", W55°52'00"
Sagona Island	+	N47°22'00", W55°47'50"
Bonne Bay	+	N47°38'50", W56°14'50"
Bay d'Espoir	+	N47°41'50", W56°07'00"
Nancy's Cove	–	N47°35'00", W55°43'30"
(No <i>Elachista</i>)		

tetraoxide and 0.1 M sodium cacodylate in MFSW. Specimens were dehydrated in an ethanol series, critical point dried, mounted on sticky carbon stubs grounded with carbon cement, and sputter coated with gold. Larvae were observed in a Joel JSM-5300 microscope at 15 kV.

Thirty larvae were separated from their host and placed in seawater in 60 mm diameter plastic Petri dishes. Individual larvae were placed equidistant (ca. 1 cm) from similarly sized clumps of four seaweeds commonly epiphytic on *Ascophyllum*: *Elachista*, *Vertebrata lanosa* (L.) Christensen [previously *Polysiphonia lanosa* (L.) Tandy], *Pilayella littoralis* (L.) Kjellmann or *Spongonema tomentosum* (Hudson) Kützing. In each trial, *Elachista* and two other species were used. Larval movement was observed over 60 min to determine if host selection occurred. In other experiments, individual larvae were placed in clumps of various species and their movement observed over 60 min.

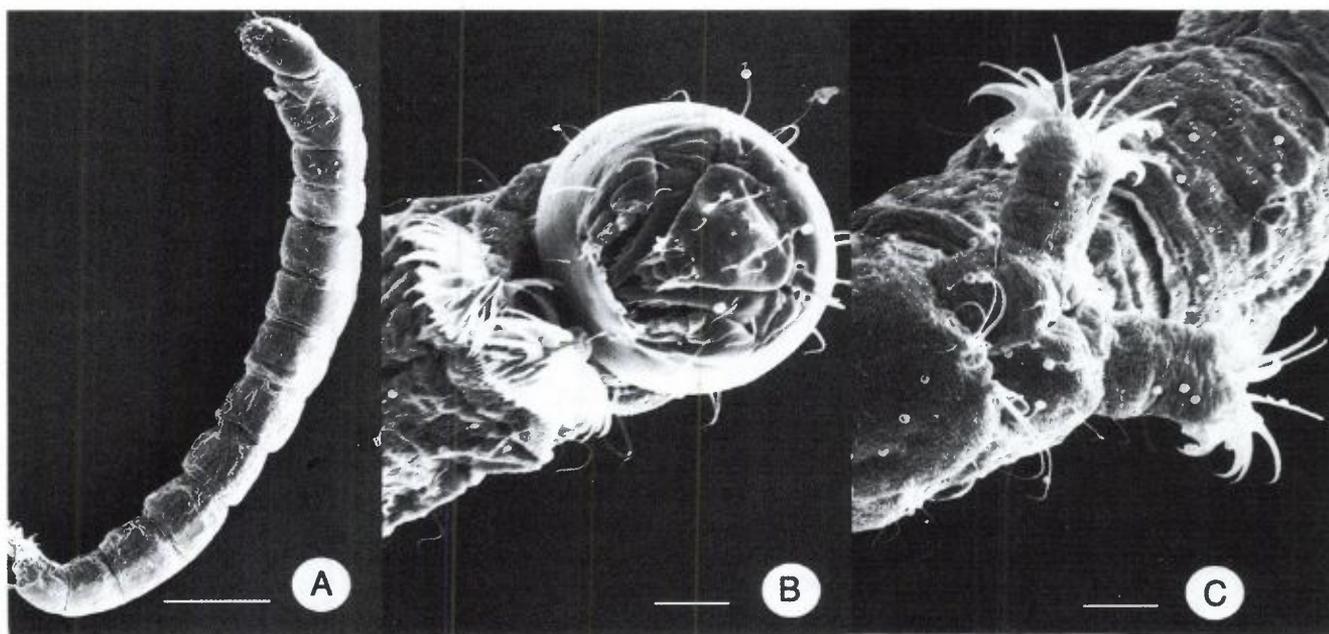


Figure 1. Scanning electron micrographs of *Halocladius variabilis*. A. Lateral view of larva; anterior end at top. Scale bar = 500 μm . B. Anterior end showing head capsule and mouthparts. Scale bar = 100 μm . C. Ventral view of larval posterior showing the two prolegs. Scale bar = 100 μm .

3. Results

Geographic distribution, host specificity and density

Halocladius larvae (Fig. 1) were associated only with *Elachista* (Fig. 2). Other common epiphytes of *Ascophyllum* included the red alga *Vertebrata lanosa*, and the brown algae *Pilayella littoralis* and *Spongonema tomentosum*. *Halocladius* was not associated with these hosts despite extremely high densities of the insect during the summer (10,000–169,000 m^{-2}). These high densities were associated with the abundance of *Elachista* that has densities of 5,000–35,000 m^{-2} during July–August at Drum Head. *Halocladius* was also associated with *Elachista* epiphytic on *Ascophyllum* at other sites in Nova Scotia (Table 1). Although both *Elachista* and *Ascophyllum* are abundant in the Bay of Fundy, at four sites over a geographic range of at least 200 km, *Halocladius* was absent.

Larval distribution in host and movement

The numerous, unbranched assimilatory filaments and the dense intertwined medullary filaments of the host provided a habitat for larvae of *Halocladius*. The basal diameter of the host ranged from several mm in diameter to several centimeters where multiple individuals of *Elachista* had coalesced. Larvae were not conspicuous at low tide, being well hidden within the basal filaments of *Elachista*. Larvae



Figure 2. Portion of single frond of *Ascophyllum nodosum* with numerous plants of *Elachista fucicola* epiphytic on upper portions of branches. Scale bar = 20 mm.

did not become detached from their substratum in the laboratory and sorted on trays or in dishpans filled with seawater. Most larvae were found only by teasing apart the host thallus with needles and forceps. Larvae moved from

the basal medullary tissue to the assimilatory filaments in the aquaria and in Petri dishes only when the entire plant was covered with seawater. Larvae did not form tubes and simply burrowed among the loosely aggregated and intertwining (i.e. syntagmatic) basal filaments of the host.

Larval movement was observed in isolated thalli of *Elachista* when larvae moved onto assimilatory filaments of the host thallus, or they were manually placed on the filaments. Larvae moved along single filaments by alternately attaching and detaching appendages at anterior and posterior ends of the organism, proceeding with a caterpillar-like locomotion where only the middle portion of the body was raised above the filament surface. The mouthparts were continuously active as larvae appeared to forage on the numerous epiphytic diatoms. The elongate cells of the diatoms were usually attached at one end, or with a short stalk, directly to the filament surface and projected perpendicular to the filament axis into the surrounding medium. Larvae that were removed from their host and placed in seawater tended to curl and uncurl, and normal movement was precluded.

Adults, egg masses and pupae

Only two adult *Halocladius* were found: one emerged from the *Elachista* in the laboratory aquarium, and the second was found in a pan of *Ascophyllum* that was being sorted. Only seven egg masses were observed; these were only associated with *Elachista* and buried deep in the medullary filaments. Pupae were more common, although only observed during July–August. Again, pupae were buried deep in the medullary filaments and were not apparent without dissection of the host. Neither pupae nor egg masses were observed during routine observations of other epiphytic algae on *Ascophyllum*.

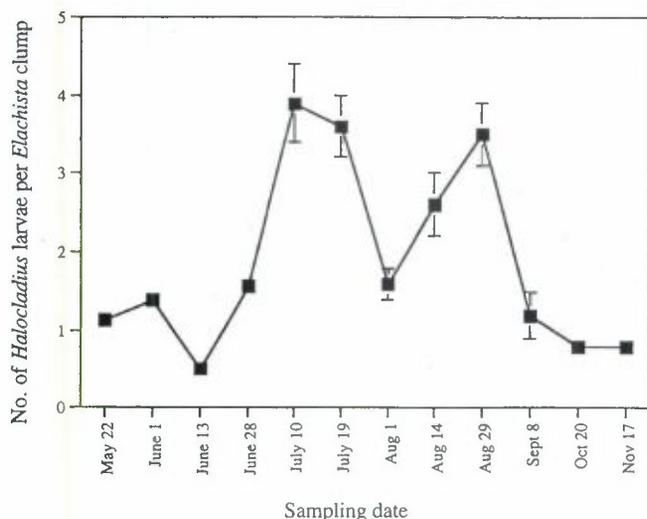


Figure 3. Numbers of larvae of *Halocladius variabilis* per thallus of *Elachista fucicola* from May to November 2001 at Drum Head.

Elachista and larval density

From late June until September, 83% of over 1,500 thalli of *Elachista* from Drum Head had at least one larva. Up to 17 larvae were present per host thallus with peak numbers occurring in mid-July (3.9 ± 0.5 ; mean \pm S.E.) and mid-August (3.5 ± 0.4) (Fig. 3). The two peaks likely resulted from two periods of egg hatching following emergence of adults in July and August. Larvae were typically very small (<2 mm long) when large numbers were present. Large larvae at the beginning of summer were more typically solitary and found in the large, overwintering *Elachista* thalli. A new cohort of *Elachista* was initiated during mid-May, and most of these thalli seemed to persist until September when numbers conspicuously declined. Biomass determinations of *Elachista* with and without larvae showed a significant difference in dry weight, with thalli hosting insects being twice as large as those without insects (10 ± 11 mg with larvae versus 5 ± 3 mg without larvae, significant at $p < 0.05$). In addition, there was a significant correlation ($r = 0.44$, $p < 0.05$) between larval numbers and host thallus weight.

Host selection by larvae

Larvae showed a limited ability to select *Elachista* over other hosts. Of the 30 independent runs where single larvae were offered a simultaneous choice of three algal species, larvae selected *Elachista* nine times (30%). The four other species were selected a combined total of only 13 times (43%). Larvae did not succeed in finding a host within the 1 h experimental period in the remaining 8 trials (27%). These individuals tended to curl and uncurl in place or simply did not move. The latter were still living and actively resumed movement when prodded. When a larva arrived at a host it remained there, regardless of host species. In addition, larvae placed in a given host showed no propensity for leaving that host and moving to *Elachista* or any other species.

4. Discussion

The symbiosis described here between a marine chironomid and an intertidal marine alga may be more common than suspected previously. There are other reports from the taxonomic literature giving apparent associations in which the insect species appears to be restricted to a particular species or group of similar algal species. For example, the chironomids *Telmatogeton sancti-pauli* (Schiner) and *T. minor* (Kieffer) are described from *Porphyra* spp. (Hesse, 1934) and *T. japonicus* (Tokunaga) is described from *Enteromorpha*, *Ulva*, and *Monostroma* (Tokunaga, 1935; P.S. Cranston, pers. obs.). A number of additional examples of possible host specificity are known (review by Hashimoto, 1976). These associations may simply reflect

microhabitat architecture and there is no evidence for a mutualistic or commensal symbiosis. Thus the association may be fortuitous based on local ecology or lack of extensive sampling of potential host species. The primary basis for the association of *Halocladius* with *Elachista* rather than other common epiphytes (e.g. *Vertebrata* and *Pilayella*) may be the soft tissue into which the adults can immerse their egg masses without risk of the eggs being washed away. In addition, the basal tissue and the host pit of *Elachista* appear to be much better refuges from predators for the larvae than other hosts (Deckert and Garbary, 2005a).

Our collections in Nova Scotia at four sites separated by at least 400 km of coastline show a consistent interaction between larvae of *Halocladius* and thalli of *Elachista* that was found also in our collections from Newfoundland. Coupled with the consistency of the association over an intensive six months of collections at Drum Head, we suggest that the association forms a regular part of the life history adaptation of *Halocladius* on rocky intertidal shores on the Atlantic coast of Nova Scotia. Johnson and Scheibling (1987) reported an unnamed dipteran larva to be common from the epifauna of *Ascophyllum* and *Fucus vesiculosus* at another rocky intertidal site in Nova Scotia where *Elachista* was a dominant epiphyte. This insect was most likely *Halocladius*.

Halocladius variabilis has a wide distribution that includes northern Europe, and the western North Atlantic and Arctic Oceans (Hirvenoja, 1973; Colbo, 1996). If a mutualistic symbiosis has evolved on the Atlantic coast of Nova Scotia and southern Newfoundland between *Halocladius* and *Elachista*, it is not an obligate relationship even in eastern Canada. Colbo (1996) reported *H. variabilis* associated with filamentous algae, particularly *Pilayella littoralis* from eastern Newfoundland. This account might also include *Elachista* since both are common epiphytes on *Ascophyllum* and can be confused by non-specialists. However, in Prince Edward Island, Giberson et al. (2001) found seven adult *H. variabilis* in a salt marsh, a habitat in which *Elachista* is unlikely. In Europe, *E. fucicola* is typically epiphytic on *Fucus vesiculosus* and is rarely on *Ascophyllum* (Fletcher, 1987). Unfortunately, only adult insects were examined by Giberson et al. (2001); thus the ecology of the larval stages was not considered. Oliver et al. (1990) recorded *H. variabilis* from Hudson Bay on the coast of Manitoba and Greenland without reference to algal hosts. *Ascophyllum* is absent in Hudson Bay (Lee, 1980), so the association with *Elachista* cannot be established in Manitoba. The wide geographic distribution and the habitat diversity of *H. variabilis* suggest a highly adaptable species that can respond to local opportunities. It would be of interest to study the extent of genetic distinction between the symbiotic populations from rocky shores and those from salt marshes.

Unlike the majority of chironomids that are microdetritivores or predators (Neumann, 1976; Pinder, 1986), the larvae of *Halocladius* are herbivorous. This is

consistent with the grazing by other chironomid larvae on rocky shores in California (Robles and Cubit, 1981; Cubit, 1982). The principle food of *Halocladius* appears to be the diatoms epiphytic on the assimilatory filaments of *Elachista*. There is no evidence that the *Halocladius* larvae cause any damage to the *Elachista* either by their feeding activity on the surface of assimilatory filaments or by their burrowing among the medullary filaments of their host.

Ascophyllum is the dominant intertidal seaweed of intertidal rocky shores in the cold temperate North Atlantic Ocean. It is long-lived with individual fronds often surviving 5–20 years or more (Baardseth, 1970). Several symbionts have been described including the mutualistic endophytic fungus *Mycophycias ascophylli* (Kohlmeyer and Kohlmeyer, 1972; Garbary and MacDonald, 1995; Garbary and London, 1995; Garbary and Deckert, 2001; Deckert and Garbary, 2005b), the commensal red algal epiphyte, *Vertebrata lanosa* (Garbary et al., 1991; Tian and Garbary, 1992; Garbary et al., 2005), and the endophytic diatom, *Navicula endophytica* Hasle (Hasle, 1972). The long lifespan of *Ascophyllum* and its high abundance in Nova Scotia (Cousens, 1984) make this species an ideal host for the evolution of symbioses.

Elachista is an abundant epiphyte on *Ascophyllum* in Nova Scotia. It is generally considered benign; however, Deckert and Garbary (2005a) showed that the rhizoids of *Elachista* penetrate deep into the host and form a pit-like chamber. These pits may weaken the host thallus and provide sites for breakage. This is consistent with the fact that thalli of *Elachista* often terminate broken branches of *Ascophyllum*. It is possible that the activity of the larvae may also contribute to damage to the *Ascophyllum* by enlarging the thallus cavities or contributing to the growth of *Elachista*. Thus, if *Halocladius* is promoting the growth of *Elachista*, *Halocladius* may be contributing to an indirect parasitism of its ultimate *Ascophyllum* host.

The symbiosis of *Halocladius* and *Elachista* may be restricted to the western Atlantic and is common in southern Newfoundland and the Atlantic coast of Nova Scotia. Although *E. fucicola* is common on rocky shores in Europe, it is typically epiphytic on *Fucus* spp. rather than on *Ascophyllum* (Fletcher, 1987). Whereas *Fucus* spp. may be perennial, fronds typically do not have the long lifespan of *Ascophyllum*. This might explain the occurrence of the symbiosis only in the western Atlantic. Both *Ascophyllum* and *Elachista* are abundant in the Bay of Fundy; however, *Halocladius* was not found at the four rocky shores sampled.

Elachista is likely an ideal host for the slow-moving larvae of *Halocladius*. The dense mass of intertwining medullary filaments that comprise the non-photosynthetic tissue of *Elachista* (Fletcher, 1987) is amenable to larval burrowing, and thus provides a refuge from predators. Based on a 75 μm diameter and a 15 mm length, each assimilatory filament provides over $3.5 \times 10^6 \mu\text{m}^2$ of surface area (surface area = $\pi d h$). With hundreds of assimilatory filaments per thallus of *Elachista*, the potential surface area

Table 2. Costs and benefits in the interactions among the four species or groups involved in the symbiosis: *Ascophyllum nodosum*, *Elachista fucicola*, *Halocladius variabilis*, and diatoms. Interactions given from perspective of first named taxon.

Interaction	Costs	Benefits
<i>Ascophyllum</i> and <i>Elachista</i>	<ul style="list-style-type: none"> - Parasitism by epiphytic <i>Elachista</i> with its host via eroding rhizoidal base; inducement of thallus breakage - Parasitism of <i>Elachista</i> exacerbated by burrowing of <i>Halocladius</i> - <i>Elachista</i> provides nutrient shadow for host 	<ul style="list-style-type: none"> - None apparent
<i>Elachista</i> and <i>Ascophyllum</i>	<ul style="list-style-type: none"> - None apparent 	<ul style="list-style-type: none"> - Long-lived and abundant substratum - ?Nutrient absorption from host
<i>Elachista</i> and <i>Halocladius</i>	<ul style="list-style-type: none"> - ?Damage from burrowing larvae 	<ul style="list-style-type: none"> - Grazing of epiphytic diatoms - ?Provision of increased nitrogen resources via insect feces
<i>Halocladius</i> and <i>Elachista</i>	<ul style="list-style-type: none"> - None apparent 	<ul style="list-style-type: none"> - Refuge from predators - Host provides 'farm' for diatom food supply
<i>Elachista</i> and diatoms	<ul style="list-style-type: none"> - Light and nutrient shadow from diatom fouling 	<ul style="list-style-type: none"> - None apparent
Diatoms and <i>Elachista</i>	<ul style="list-style-type: none"> - None apparent 	<ul style="list-style-type: none"> - Extensive surface area for growth - Increased light availability - Improved nutrient environment

per thallus for diatom colonization is at least $10^8 \mu\text{m}^2$. Given the densities of *Elachista* at our site (5,000–35,000 m^{-2} during June–July), this provides a huge potential substratum for diatom growth and grazing area for *Halocladius* in the mid-intertidal zone. *Halocladius* thus plays an equivalent role to chironomid grazers in freshwater (e.g. Botts, 1993) and many arthropod mesoherbivores in the marine benthos (Brawley, 1992; Williams and Seed, 1992). It would be of interest to compare the role of *Halocladius* with amphipods (cf. Duffy and Hay, 2000) in maintaining overall community structure and host epiphyte interactions among diatoms, *Elachista*, and *Ascophyllum*.

Our experiments on host selection by larvae suggest that this life history stage has only limited sensory or motor skills to select *Elachista* over other algal hosts. Selection of *Elachista* thalli likely occurs at oviposition. The egg masses observed had 25–50 eggs within the egg capsule which hatch equal sized larvae ca. 0.2 mm long. After hatching, larvae move out of egg mass into the surrounding area. *In situ*, there must be severe competition for space and food for these juveniles. Reduction from the large numbers that hatch from a single egg capsule to the 1–10 larvae present in most thalli of *Elachista*, might be associated with mortality on several fronts: 1) predation by vertebrates and invertebrates, 2) intraspecific competition leading to starvation, and 3) dislodging of small larvae. The latter might occur in *Ascophyllum* beds during high tide when wave action is sufficient to dislodge feeding larvae. Although average densities of *Elachista* during the summer may be only about 5,000 m^{-2} , their distribution is highly clumped, with some *Ascophyllum* fronds having many *Elachista* (e.g. Fig. 2) and other fronds having few or none. During wave action many thalli would be moving against

each other, and this would facilitate dislodgement or dispersal of larvae from one host thallus to another when they are feeding in the assimilatory filaments of the host.

Bronstein (2001) suggested that mutualisms should be considered in an evolutionary perspective by determining the costs as well as the benefits of the interactions. Using this approach with respect to *Elachista* and *Halocladius* (Table 2), it is difficult to determine where costs are involved from the perspective of *Elachista*. This association is of considerable interest in that at least two photosynthetic partners are involved (i.e. diatoms, *Elachista*), one of which might be regarded as a parasite (i.e. the diatoms) of the other photosynthetic partner as a consequence of light and nutrient absorption (Wahl, 1989), and that potential relief from this parasitism is given by the herbivore (i.e. *Halocladius*).

The abundance of *Halocladius* in the rocky intertidal zone and its host specificity to *Elachista* demonstrate that this is at least a commensal symbiosis. Circumstantial evidence from observations on the natural history of the association suggest that this is a mutualistic symbiosis that needs to be further explored. On a larger scale, the diatom-*Halocladius*-*Elachista* interactions are part of a symbiotic community hosted by *Ascophyllum* that includes an obligate marine fungus and an obligate epiphytic red alga (Garbary and Deckert, 2001). This community forms a complex marine symbiosis that is the most conspicuous feature of marine shores on the Atlantic coast of Nova Scotia.

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REFERENCES

- Baardseth, E. 1970. Synopsis of biological data on knobbed wrack. *F.A.O. Fisheries Synopsis* **38**: 1-46.
- Botts, P.S. 1993. The impact of small chironomid grazers on epiphytic algal abundance and dispersion. *Freshwater Biology* **30**: 25-33.
- Brawley, S.H. 1992. Mesoherbivores. In: *Plant-Animal Interactions in the Marine Benthos*. D.M. John, S.J. Hawkins, and J.H. Price, eds. Clarendon Press, Oxford, Systematics Association Special Vol. No. 46, pp. 235-263.
- Bronstein, J.L. 2001. The costs of mutualism. *American Zoologist* **41**: 825-839.
- Colbo, M.H. 1996. Chironomidae from marine coastal environments near St. John's, Newfoundland, Canada. *Hydrobiologia* **318**: 117-122.
- Cousens, R. 1984. Estimation of annual production by the intertidal brown alga *Ascophyllum nodosum* (L.) Le Jolis. *Botanica Marina* **27**: 217-227.
- Cubit, C. 1982. Disturbance and predation in an assemblage of herbivorous Diptera and algae on rocky shores. *Oecologia* **54**: 23-31.
- Dawes, C.J. 1998. *Marine Botany*, 2nd ed. John Wiley, New York, 480 pp.
- Deckert, R. and Garbary, D.J. 2005a. *Ascophyllum* and its symbionts. VIII. Interactions among *Ascophyllum nodosum* (Phaeophyceae), *Mycophycias ascophylli* (Ascomycetes) and *Elachista fucicola* (Phaeophyceae). *Algae* **20** (in press).
- Deckert R. and Garbary D.J. 2005b. *Ascophyllum* and its symbionts. VI. Microscopic characterization of the *Ascophyllum nodosum* (Phaeophyceae), *Mycophycias ascophylli* (Ascomycetes) symbiotum. *Algae* **20**: 225-232.
- Duffy, J.E. and Hay, M.E. 2000. Strong impacts of grazing amphipods on the organization of a benthic community. *Ecological Monographs* **70**: 237-263.
- Fletcher, R.L. 1987. *Seaweeds of the British Isles*. Volume 3, Fucophyceae (Phaeophyceae) Part 1. British Museum (Natural History), London, 359 pp.
- Garbary, D.J., Burke, J., and Tian, L. 1991. The *Ascophyllum/Polysiphonia/Mycosphaerella* symbiosis II. Aspects of the ecology and distribution of *Polysiphonia lanosa* in Nova Scotia. *Botanica Marina* **34**: 391-401.
- Garbary, D.J. and Deckert, R. 2001. Three part harmony - *Ascophyllum* and its symbionts. In: *Symbiosis: Processes and Model Systems*. J. Seckbach, ed. Kluwer, The Netherlands, pp. 309-321.
- Garbary, D.J., Deckert, R., and Hubbard, C. 2005. *Ascophyllum* and its symbionts. VII. Three-way interactions among *Ascophyllum nodosum* (Phaeophyceae), *Mycophycias ascophylli* (Ascomycetes) and *Vertebrata lanosa* (Rhodophyta). *Algae* (in press).
- Garbary, D.J. and MacDonald, K. 1995. The *Ascophyllum/Polysiphonia/Mycosphaerella* symbiosis IV. Mutualism in the *Ascophyllum/Mycosphaerella* interaction. *Botanica Marina* **38**: 221-225.
- Garbary, D.J. and London, J.F. 1995. The *Ascophyllum/Polysiphonia/Mycosphaerella* symbiosis V. Fungal infection protects *A. nodosum* from desiccation. *Botanica Marina* **38**: 529-533.
- Giberson, D.J., Bilyj, B., and Burgess, N. 2001. Species diversity and emergence patterns of nematocerous flies (Insecta: Diptera) from three coastal salt marshes in Prince Edward Island. *Estuaries* **24**: 862-874.
- Goldfinch, A.C. and Carman, K.R. 2000. Chironomid grazing on benthic microalgae in a Louisiana salt marsh. *Estuaries* **23**: 536-547.
- Gullan, P.J. and Cranston, P.S. 2004. *Insects: An Outline of Entomology*, 3rd ed. Blackwell Science, Oxford, 502 pp.
- Hashimoto, H. 1976. Non-biting midges of marine habitats (Diptera: Chironomidae). In: *Marine Insects*. 1. Cheng, ed. North Holland Publishing Company, Amsterdam, pp. 377-414.
- Hasle, G.R. 1968. *Navicula endophytica* sp. nov., a pinnate diatom with an unusual mode of existence. *British Phycological Bulletin* **3**: 475-480.
- Hesse, A.J. 1934. Contributions to a knowledge of South African marine Clunionine-chironomids. *Transactions of the Royal Entomological Society of London* **82**: 27-40.
- Hirvenoja, M. 1973. Revision der Gattung *Cricotopus* vander Wulp und ihrer Verwandten (Diptera: Chironomidae). *Annales Zoologicae Fennicae* **101**: 1-363.
- Johnson, S.C. and Scheibling, R.E. 1987. Structure and dynamics of epifaunal assemblages on intertidal macroalgae *Ascophyllum nodosum* and *Fucus vesiculosus* in Nova Scotia, Canada. *Marine Ecology Progress Series* **37**: 209-227.
- Kohlmeyer, J. and Kohlmeyer, E. 1972. Is *Ascophyllum nodosum* lichenized? *Botanica Marina* **15**: 109-112.
- LaSalle, M.W. and Bishop, T.D. 1987. Seasonal abundance of aquatic Diptera in two oligohaline tidal marshes in Mississippi. *Estuaries* **10**: 303-315.
- Lee, R.K.S. 1980. *A Catalogue of the Marine Algae of the Canadian Arctic*. National Museums of Canada, Ottawa, Publications in Botany, No.9, 82 pp.
- Levinton, J.S. 2001. *Marine Biology, Function, Biodiversity, Ecology*, 2nd ed. Oxford University Press, Oxford, 515 pp.
- Little, C. and Kitching J.A. 1996. *The Biology of Rocky Shores*. Oxford University Press, Oxford, 240 pp.
- Neumann, D. 1976. Adaptations of chironomids to intertidal environments. *Annual Review of Entomology* **21**: 387-414.
- Nybakken, J.W. 2001. *Marine Biology, An Ecological Approach*, 5th ed. Benjamin Cummings, San Francisco, 516 pp.
- Oliver, D.R., Dillion, M.E., and Cranston, P.S. 1990. *A Catalog of the Nearctic Chironomidae*. Research Branch, Agriculture Canada, Ottawa, Publication 1857B, 89 pp.
- Pinder, L.C.V. 1986. Biology of freshwater Chironomidae. *Annual Review of Entomology* **31**: 1-23.
- Robles, C.D. and Cubit, J. 1981. Influence of biotic factors in an upper intertidal community: Dipteran larvae grazing on algae. *Ecology* **62**: 1536-1547.
- Tian, L. and Garbary, D.J. 1992. The *Ascophyllum/Polysiphonia/Mycosphaerella* symbiosis III. Experimental studies on the interactions between *P. lanosa* and *A. nodosum*. *Botanica Marina* **35**: 341-349.
- Tokunaga, M. 1935. Chironomidae from Japan IV. On the early stages of a marine midge *Telmatogeton japonicus* Tokunaga. *Philippine Journal of Science* **57**: 491-511.
- Wahl, M. 1989. Marine epibiosis. I. Fouling and antifouling: some basic aspects. *Marine Ecology Progress Series* **58**: 175-189.

- Williams, D.D. 1999. Why are there so few insects in the sea? *Trends in Entomology* 2: 63-70.
- Williams, D.D. and Williams, N.E. 1998. Aquatic insects in an estuarine environment: densities, distribution and salinity tolerance. *Freshwater Biology* 39: 411-421.
- Williams, C.A. and Seed, R. 1992. Interactions between macrofaunal epiphytes and their host. In: *Plant-Animal Interactions in the Marine Benthos*. D.M. John, S.J. Hawkins, and J.B. Price, eds. Clarendon Press, Oxford, Systematics Association Special Vol. No. 46, pp. 189-211.