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Halocladius variabilis (Diptera: Chironomidae): a marine insect symbiotic with seaweeds from the White Sea, Russia

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The commensal (and possibly mutualistic) symbiosis between the marine chironomid, Halocladius variabilis*, and brown algal epiphytes of* Fucus vesiculosus *and* Ascophyllum nodosum *is described for the first time from Europe, based on field studies from the White Sea, Russia. While the primary host,* Elachista fucicola*, and the secondary host,* A. nodosum*, are the same as in eastern Canada where the symbiosis was first described, White Sea populations have a wider range of primary hosts that include* Pylaiella littoralis *and* Dictyosiphon foeniculaceus. *About 64% of* E. fucicola *thalli on* A. nodosum *in the low intertidal zone were colonized. Significantly lower frequencies were found on* E. fucicola *when the latter was epiphytic on* F. vesiculosus *at the same tidal height or on either secondary host when they were in the subtidal zone. For a given tidal height, or secondary host, frequency of* H. variabilis *was reduced on* P. littoralis *and further reduced on* D. foeniculaceus. *We suggest that subtidal populations are colonized by dispersal of larvae from the intertidal zone on to suitable substrata, and that there is limited potential for these individuals to reach the intertidal zone as adults for reproduction.*

Keywords: *Chironomidae*, Elachista, Halocladius, marine insects, White Sea

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INTRODUCTION

Despite their extreme species richness in terrestrial environments, insects are poorly represented in marine habitats and their occurrence on rocky shores has been previously underestimated (Neumann, 1976; Gullan & Cranston, 2004). The few strictly marine species are rarely conspicuous members of this environment, and terrestrial species are rarely abundant in the intertidal zone except in salt marshes and estuaries (e.g. Garbary *et al.*, 2004). Consequently, insects are typically ignored in general textbooks of marine biology (e.g. Levington, 1995). Nevertheless, marine insects can be abundant (e.g. Cubit, 1982; Neumann, 1986; Johnson & Scheibling, 1987; Garbary *et al.*, 2008). The general lack of consideration given these organisms may be associated with their small size, often cryptic eclosion times (e.g. Neumann, 1986) or habitats associated with seaweeds in the upper intertidal zone (e.g. Robles & Cubit, 1981; McAllen, 1999) and short adult life spans (Neumann, 1976).

Among the most abundant and well represented of insects in saline environments is an array of non-biting midges (family Chironomidae), of which there are 15 genera and at least 50 described species (Hashimoto, 1976; Neumann, 1976; Colbo, 1996). The chironomid genus *Halocladius* (Hirvenoja, 1973) has five species, all of which are halophilic, and of which *H. variabilis* (Staeger, 1839) is the most widely distributed. This species has been extensively reported from the Holarctic of eastern and northern Canada to northern Europe and the Mediterranean and Black Seas (e.g. Hirvenoja, 1973, 1975; Santhakumaran *et al.*, 1984; Colbo, 1996; Garbary *et al.*, 2005b; Hirvenoja *et al.*, 2006). The species may be best known as a larval stage from eastern Canada where numerous collections of larvae suggest a commensal and possibly mutualistic symbiosis with marine intertidal algae, in particular *Elachista fucicola* (Velley) Areschoug (Garbary *et al.*, 2005a, 2008). In this symbiosis the insect feeds on the fouling diatoms that are abundant on its host, and may be delivering nutrients via faecal material. In the northern Baltic Sea the adult phase is best known and numerous adults have been observed (e.g. Hirvenoja *et al.*, 2006). These observations, along with Santhakumaran *et al.* (1984) suggested much wider habitat utilization by *Halocladius* than was assumed by Neumann *et al.* (1997) who placed larval habitat in the mid to high intertidal zones on rocky shores.

In 2006, one of us (E.T.) observed a single larva of *H. variabilis* associated with *E. fucicola* growing on *Ascophyllum nodosum* (Linnaeus) Le Jolis collected from the White Sea. In light of the previous observations from Nova Scotia of *H. variabilis* and *E. fucicola* (Garbary *et al.*, 2005b, 2009), we undertook the present study to determine if the symbiosis characterized from eastern Canada was also present in the White Sea. In addition, we examined whether differences in the ecology of the primary and secondary host were also reflected in differences in the symbiotic association.

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MATERIALS AND METHODS

Study sites

All observations were made in the Keret Archipelago (Kandalaksha Bay, White Sea) in August 2007 (Table 1). The Keret Archipelago has a tidal amplitude of 1.3 to 1.8 m for neap and spring tides, respectively, with surface water temperature reaching 17°C. The intertidal zones typically have extensive populations of *Fucus vesiculosus* Linnaeus (see AlgaeBase, Guiry & Guiry 2008 for additional nomenclatural details on algal taxa), and the shallow subtidal zone is typically occupied by *Ascophyllum nodosum* (Zinova, 1953; Vozzhinskaya, 1986). Three other fucoids were also observed in our study (Table 1): *F. serratus* Linnaeus, *F. distichus* Linnaeus and *Pelvetia canaliculata* (Linnaeus) Decaisne and Thuret; however *H. variabilis* was not observed with these secondary hosts.

Both *F. vesiculosus* and *A. nodosum* had extensive populations of filamentous or finely branched brown algae that included *E. fucicola*, *Pylaiella littoralis* (Linnaeus) Kjellman (most commonly) and *Dictyosiphon foeniculaceus* (Hudson) Greville and *Ectocarpus* sp. (less commonly). Algal nomenclature follows Guiry & Guiry (2008).

The study sites (Table 1) were all rocky shores of moderate to high wave exposure and a surface salinity of 22–24 ppt. We examined four shore zones at each site (from shallow subtidal to high intertidal) along a 50–70 m extent of shoreline. At each tidal height ten fronds of the fucoids, *F. vesiculosus* and *A. nodosum* with conspicuous epiphytic populations were selected haphazardly and returned to the laboratory. Where the two fucoids overlapped in the low intertidal zone and subtidal zones ten fronds of each species were collected.

Algal epiphytes from the fucoid fronds were examined with a dissecting microscope. Each frond bore 5 to 15 epiphytic algal thalli that were identified to species and scored for occurrence and number of chironomid larvae or pupae. Data analysis was carried out using STATISTICA 7.1 (StatSoft Inc., USA). We used a nested ANOVA design with 'secondary host (macrophyte)' nested in 'shore zone' and 'primary host (epiphyte)' in 'shore zone' and 'secondary host'. As there was no significant difference in larval distribution between sites (Table 3) we grouped data from all sites for comparison

Table 1. Study sites in the White Sea where *Halocladius variabilis* was collected along with distribution of fucoid species and their epiphytes.

Location	Latitude and longitude	Position on shore	Primary fucoid species	Primary brown algal epiphytes
Site 1	66° 17′ 28.76″N; 33° 40′ 03.46″E	Shallow subtidal	*A. nodosum**, *F. vesiculosus*, *F. serratus*	*P. littoralis, E. fucicola, Ectocarpus* spp., *Dictyosiphon foeniculaceus*
(Srednii Island, Yushkovka Bay)		Low intertidal	*F. vesiculosus, A. nodosum*	*E. fucicola, P. littoralis, D. foeniculaceus, Ectocarpus* sp.
High exposure, salinity 22 ppt		Mid-intertidal	*F. vesiculosus*	*E. fucicola*
		High intertidal	*F. vesiculosus*	No epiphytes
Site 2	66° 18′ 35.20″N; 33° 39′ 20.58″E	Shallow subtidal	*A. nodosum, F. vesiculosus, F. serratus*	*P. littoralis, E. fucicola, Ectocarpus* sp., *D. foeniculaceus*
(Keret Island, Sukhaya Salma Strait)		Low intertidal	*F. vesiculosus, A. nodosum,*	*E. fucicola, P. littoralis, D. foeniculaceus Ectocarpus* sp.
Moderate exposure, salinity 22 ppt		Mid-intertidal	*F. vesiculosus, A. nodosum*	*E. fucicola, P. littoralis*
		High intertidal	*F. vesiculosus*	*P. littoralis*
Site 3	66° 18′ 30.57″N; 33° 55′ 11.68″E	Shallow subtidal	*A. nodosum, F. serratus, F. vesiculosus*	*P. littoralis, E. fucicola*
(Sedlovataya Luda Island)		Low intertidal	*F. vesiculosus, A. nodosum*	*E. fucicola, P. littoralis, D. foeniculaceus, Ectocarpus* sp.
High exposure, salinity 24 ppt		Mid-intertidal	*F. vesiculosus*	*E. fucicola, P. littoralis*
		High intertidal	*Pelvetia canaliculata, F. vesiculosus, F. distichus*	No epiphytes

*, for all species names in full, see text.

Table 2. Distribution of larvae of *Halocladius variabilis* on different algae in intertidal and shallow subtidal zones in the Keret Archipelago. Figures indicate means ± standard errors.

Primary algal host	Secondary macrophyte host	Host thalli with chironomid larvae in different shore zones, %			
		Shallow subtidal	Low intertidal	Mid-intertidal	High intertidal
Elachista fucicola	*F. vesiculosus**	10.1 ± 0.4	27.5 ± 1.6	18.10 ± 0.9	No epiphyte
	A. nodosum	16.7 ± 0.9	63.8 ± 3.0	No epiphyte	No macrophyte
Pylaiella littoralis	*F. vesiculosus*	7.9 ± 0.4	20.4 ± 1.4	12.8 ± 1.1	2.2 ± 0.2
	A. nodosum	7.1 ± 0.4	22.1 ± 1.0	No epiphyte	No macrophyte
Dictyosiphon foeniculaceus	*F. vesiculosus*	Not determined	Not det.	12.4 ± 0.8	Not determined
	A. nodosum	Not determined	10.1 ± 0.9	No epiphyte	No macrophyte

*, for all species names in full, see text.

Table 3. Summary of ANOVA tables for analyses of data shown in Table 2.

Variable	df	F-ratio	*P*
Site	2	0.24	0.79
Shore zone	3	229.05	<0.001
Secondary host (shore zone)	2	29.13	<0.001
Primary host (shore zone, secondary host)	7	161.39	<0.001

of larval occurrence on primary and secondary hosts. ANOVA was carried out using STATISTICA 5.5 (StatSoft Inc., USA).

Note on identification of *Halocladius variabilis*

While adults of *Halocladius variabilis* are required for definitive identification of the species, all chironomid larvae observed had morphology consistent with *H. variabilis* from eastern Canada. In addition, the paucity of chironomid species in marine habitats and the consistency of the association with filamentous brown algae (Colbo, 1996; Garbary *et al*., 2005b) as observed in eastern Canada, led us to assume that all larvae were *H. variabilis*. One other chironomid, *Cricotopus vitripennis* (Meigen, 1822), is widely distributed in the intertidal zone of the White Sea. *Cricotopus* is found in mud or with decaying algal mats, where its larvae are associated with mussel beds or with assemblages of tube-dwelling polychaetes (e.g. Khaitov *et al*., 1999).

RESULTS

The primary and secondary algal hosts were collected from three sites in the Keret Archipelago. These sites had conspicuous populations of *F. vesiculosus* and *A. nodosum* in the mid–low intertidal zone and the shallow subtidal zone (depth 1–1.5 m during the lowest tides) and these fucoids had extensive populations of brown algal epiphytes (Table 1). The two fucoids were typically in a continuous bed from the shallow subtidal to the mid intertidal zones. *Fucus vesiculosus* tended to occur in a dense band from the mid shore to the low intertidal zone. In the high intertidal zone *F. vesiculosus* cover degraded to separate beds about 0.5 m in diameter. *Ascophyllum nodosum* was common in the low intertidal zone where it was often mixed with *F. vesiculosus*, but it formed a more-or-less continuous bed to about 1.5 m below the low tide level.

Larvae of *H. variabilis* were present at every site. Larvae varied from 3 to 10 mm in length, and the smaller ones were more abundant. Each host epiphytic thallus typically had only one larva and never more than two. Egg masses were never observed. While adults were not observed, 5 pupae (8–10 mm) were found. All pupae were associated with *E. fucicola*, where they were embedded in the dense filamentous matrix at the base of the uniseriate filaments. The pupae were only found in the intertidal zone. The presence of pupae and the absence of egg masses suggests that eclosion, mating and egg laying was later in the season than our observations.

A total of ~2000 thalli of epiphytic algae representing three primary host species were scored for presence of *H. variabilis*. The primary hosts were *E. fucicola*, *P. littoralis* and *D. foeniculaceus*. *Ectocarpus* was only recorded infrequently and so was excluded from our study. These primary hosts occurred as epiphytes on the fucoid species *A. nodosum* and *F. vesiculosus* (secondary hosts). *Halocladius* was most prevalent in the low intertidal zone where it had the highest frequency on *E. fucicola* with *A. nodosum* as the secondary host and 64% of *E. fucicola* thalli had at least one larva. This was followed by *E. fucicola* on *F. vesiculosus* where 27% of thalli were colonized (Table 2). *Halocladius* on primary hosts other than *E. fucicola* was less abundant, as generally was the occurrence of the chironomid with the secondary host *F. vesiculosus*. Differences in occurrence between the three primary hosts and the two secondary hosts were significant at $P < 0.01$ (Table 3).

DISCUSSION

Our observations clearly demonstrate that the symbiosis between the marine chironomid, *H. variabilis*, and its primary host *E. fucicola* described from Canada by Garbary *et al.* (2005a, 2009) also occurs in the White Sea. The relationship in the White Sea is more flexible than that in Nova Scotia in that a greater number of primary (i.e. algae other than *E. fucicola*) and secondary (i.e. hosts other than *A. nodosum*) hosts are available to the insect, even though the highest frequency of occurrence is still retained with *E. fucicola* (i.e. 64%) and *A. nodosum*. Garbary *et al.* (2005) described a close association between *A. nodosum*, *E. fucicola* and *H. variabilis* in Nova Scotia, Canada.

The occurrence of *H. variabilis* larvae in the subtidal zone of the White Sea is unusual considering that the adult stage of the insect flies (e.g. Hirvenoja *et al*., 2006), and cannot survive immersion in seawater. The occurrence of subtidal larvae presents two difficulties. First, how can hosts become colonized if this requires egg-laying, *in situ*, by the adult? Secondly, once the larvae have pupated and then emerged, can the new adults possibly survive seawater immersion to successfully mate and then lay eggs?

The first problem might be overcome by dispersal of individual larvae from an intertidal host thallus and then becoming reattached to another host clump. Given the high densities of both fucoid fronds and their brown algal epiphytes, this is plausible. The high proportion of colonized *E. fucicola* thalli, and the fact that the majority of these thalli host only a single larva, is consistent with dispersal rather than predation as the causal factor. Thus, if predation was the primary cause of larval loss for the host, then one would expect to see a greater variation in larval numbers per host, and many more host thalli with zero larvae. Dispersal and random reattachment to other primary hosts may also explain the much lower frequency on *P. littoralis* and *D. foeniculaceus*. An alternative explanation for the reduction to 1–2 larvae per host is the possibility of sibling cannibalism. This has been reported in the freshwater insect *Hydropsyche slossonae* (Banks, 1905) where there is a 92% loss of 1st instar larvae as a consequence of sibling cannibalism (Willis & Hendricks, 1992).

It is also possible that during extreme neap tides in August the upper portions of the *A. nodosum* fronds with their epiphytic clumps may be floating at the surface, and this provides sufficient opportunity for both egg-laying and emergence of the adults. Subtidal populations of *H. variabilis* were reported previously (Santhakumaran *et al.*, 1984); however, no explanations were offered here as to the origin of the larvae. The winged nature of *Halocladius* adults contrasts with the unwinged genera *Pontomyia* (Edwards, 1926) and *Clunio* (Haliday, 1855). These genera have extensive subtidal populations and the unwinged or flightless adults eclose, mate and lay eggs on the sea surface (Tokunaga, 1932; Cheng & Collins, 1980; Neumann, 1986). Since the egg masses we observed in Nova Scotia were deeply immersed in the filaments of *E. fucicola*, this must be an active process carried out by adult *Halocladius*.

While not representing obligate associations, the primary relationship of *H. variabilis* to *E. fucicola* and the secondary relationship to *A. nodosum* are the most prevalent in the White Sea. Symbioses involving *A. nodosum* as a host have been extensively studied and involve an obligate mutualistic association with an endophytic fungus, *Mycophycias ascophyli* (Cotton) Kohlmann & Volkmann-Kohlmeyer (Garbary & MacDonald, 1995; Garbary & London, 1995; Deckert & Garbary, 2005; Xu *et al.*, 2008), a host-specific red algal epiphyte *Vertebrata lanosa* (Linnaeus) Christensen (Garbary *et al.*, 1991, 2005a; Tian & Garbary, 1992), as well as facultative symbioses with algae including *E. fucicola* (review by Garbary & Deckert, 2001). While Johnson & Scheibling (1987) did not identify *H. variabilis* specifically, the abundant chironomid associated with epiphytes of *Fucus* and *Ascophyllum* in their study from the south shore of Nova Scotia is likely to be this species.

Adults of *H. variabilis* have been found on sites other than the rocky intertidal zone. These include salt marshes (Giberson *et al.*, 2001) and terrestrial habitats some distance from the seashore (Hirvenoja *et al.*, 2006). There are also occasional findings of the larvae of *H. variabilis* in fresh water habitats in northern Europe (Kuz'mina, 2001). The abundance and degree of specificity of the *H. variabilis* symbiosis with brown algal hosts suggests that this is central to the biology of the species. That numerous adults were also observed in this rocky intertidal zone of Nova Scotia in August 2007 (Garbary, unpublished observations) confirms that the insect is completing its life cycle in this habitat. The observations of alternative habitats suggest a plastic ecology on the part of *H. variabilis* or the possibility of multiple divergent races with widespread distributions.

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