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The effect of light on the settlement of the salmon louse, *Lepeophtheirus salmonis*, on Atlantic salmon, *Salmo salar* L.

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Abstract

The salmon louse, *Lepeophtheirus salmonis*, is an ectoparasitic copepod that infests both wild and farmed salmonid fish. Salmon lice are a major disease problem in the farming of Atlantic salmon, *Salmo salar* L., and the possibility of salmon lice playing a role in the decline of wild anadromous stocks has also been raised. *Lepeophtheirus salmonis* can detect a range of stimuli (pressure/moving water, chemicals and light) in the external environment. However, the response thresholds to various stimuli, and the spatial and temporal scales over which they operate in the context of host location, are largely unknown. In this context, we attempted to determine whether salmon lice copepodids settle onto hosts more effectively, or at different locations on the fish's body, under different qualities of light. Lice settlement trials were conducted under three lighting conditions; L1: unpolarized under ultraviolet A (UVA)-through visible; L2: unpolarized without UVA (control); L3: 100% linearly polarized without UVA. A dark control was also conducted. No statistically significant difference in lice settlement was found. While changes in light intensity are involved in host detection at spatial scales on the order of metres, the results presented here suggest that it is not the primary sensory modality underlying host location at smaller spatial scales (cm to mm).

Keywords: Lepeophtheirus salmonis, parasite host-finding, polarization vision, spectral reflectance, ultraviolet vision, vision.

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Introduction

The salmon louse, *Lepeophtheirus salmonis*, is an ectoparasitic copepod that infests both wild and farmed salmonid fish, mainly of the genera *Salmo*, *Salvelinus* and *Oncorhynchus* (Pike & Wadsworth 1999). Salmon lice are a major disease problem in the farming of Atlantic salmon, *Salmo salar* L., and they have been implicated in the decline of some wild anadromous stocks (e.g. Birkeland 1996; Finstad, Bjørn, Grimnes & Hvidsten 2000). *Lepeophtheirus salmonis* hatch as nauplius I larvae from egg strings carried by adult females (which are attached to the host) and immediately commence a free-swimming planktonic lifestyle. The species' life cycle consists of several larval stages – two naupliar, one copepodid and four chalimus – before passing through two pre-adult stages, which culminate in male and female host-resident adults (Johnson & Albright 1991). The copepodid is the primary infective stage; the sole purpose of this free-living larval form is to locate and attach to a suitable host. In recent years, the search for effective and long-term solutions to the problems caused by salmon lice – and other parasites of fish – has turned from delousing treatments to improving our knowledge of their biology. One aspect of this work focuses on the host-associated stimuli that parasites might use to locate and discriminate a compatible host (e.g. Buchmann & Nielsen 1999; Novales Flamarique, Browman, Bélanger & Boxaspen 2000; Buchmann & Lindenstrøm 2002; Haas, Stiegeler, Keating, Kullmann, Rabenau, Schonamsgruber & Haberl 2002; Haas 2003; Luntz 2003; Mikheev, Pasternak & Valtonen 2003, 2004).

Lepeophtheirus salmonis can detect a range of environmental and host-related stimuli – pressure/

moving water, light, salinity, temperature and semiochemicals (Wootten, Smith & Needham 1982; Bron, Sommerville & Rae 1993; Heuch & Karlsen 1997; Devine, Ingvarsdottir, Mordue, Pike, Pickett, Duce & Mordue 2000; Novales Flamarique *et al.* 2000; Ingvarsdóttir, Birkett, Duce, Mordue, Pickett, Wadhams & Mordue (Luntz) 2002a; Ingvarsdóttir, Birkett, Duce, Genna, Mordue, Pickett, Wadhams & Mordue (Luntz) 2002b; Luntz 2003). However, the response thresholds to these stimuli, and the spatial and temporal scales over which they operate in the context of host location, are largely unknown. The following is a brief overview of behavioural studies on salmon lice that are related to host location.

Heuch & Karlsen (1997) observed that copepodids (the infective stage) are sensitive to hydrodynamic cues. Vibrations of 3 Hz produced the greatest response: swimming speeds of 9 cm s^{-1} compared with a background speed of 2 cm s^{-1}. This can be interpreted as a mechanism that would facilitate contact with a potential host fish swimming nearby (Hevrøy, Boxaspen, Oppedal, Taranger & Holm 2003).

The response of *L. salmonis* to host-derived chemical stimuli appears to vary according to life stage. Adult male lice increased their swimming activity, and were attracted to, salmon conditioned water (SCW) (Ingvarsdóttir *et al.* 2002a,b). It should be noted, however, that lice were given 10 min to orient in these Y-maze trials; too long to be considered relevant in the context of host location, as a louse would never have more than a few seconds to locate and attach to a salmon swimming nearby. Copepodids, however, did not respond to numerous host chemical sources, including bile, blood, faeces/urine, mucus and skin (Bron *et al.* 1993). Nonetheless, in one way or another, fish parasites do generally respond preferentially to host-specific chemicals (e.g. Haas *et al.* 2002; Buchmann & Nielsen 1999; Buchmann & Lindenstrøm 2002; Luntz 2003).

The structure of the *L. salmonis* eye suggests that it is important for the copepodid and/or that it plays a major role in later developmental stages. The optic photoreceptor of the copepodid is comprised of a median nauplius eye consisting of two lensed dorsolateral ocelli and a single unlensed ventral ocellus. Each dorsolateral ocellus has a slightly larger maximum transverse diameter than other species reported and, thus, has a far higher eye to body length ratio (Bron & Sommerville 1998). The spectral sensitivity of the *L. salmonis* retina is unknown (but see spectral response results presented by Novales Flamarique *et al.* 2000). Numerous investigators have observed positive phototaxis behaviour in salmon lice and strong responses to both shadows and flashes of light (Wootten *et al.* 1982; Bron *et al.* 1993; Bron & Sommerville 1998; Aarseth & Schram 1999; Novales Flamarique *et al.* 2000).

The morphological basis (orthogonal microvilli) also exists for the eye of *L. salmonis* to act as a polarization (POL) detector, as has been reported for other invertebrates with virtually identical eye structure (Bron & Sommerville 1998; Wehner 1997). Further, the arrangement of the tapetal cells behind the louse ocelli (Land 1981; Bron & Sommerville 1998) could improve the efficiency of the POL detection system (Novales Flamarique & Hawryshyn 1998). In many invertebrates, and some vertebrates, polarization vision is used (in a manner analogous to colour vision) for object recognition, signal detection and discrimination, contrast enhancement and camouflage breaking (see Cronin, Shashar, Caldwell, Marshall, Cherokee & Chiou 2003; Horváth & Varjú 2004). The scales on the sides of salmon are highly reflective across the visible spectrum (Fig. 1). Thus, it is possible that they produce a distinct POL reflection – different from the background underwater POL field – that could serve as a host detection cue for the louse (*sensu* Shashar, Hagan, Boal & Hanlon 2000; Land 1991; Rowe & Denton 1997; Cronin *et al.* 2003). In an analogous manner, ultraviolet A

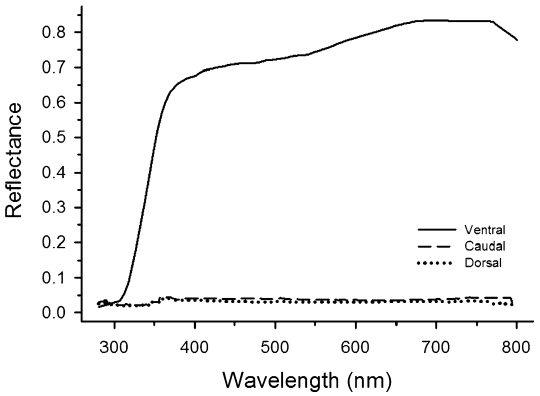

Figure 1 Spectral reflectance (280–800 nm) of the Atlantic salmon body surface from the ventral (along the lateral line groove between the pectoral and pelvic fins), dorsal (in front of the dorsal fin), and caudal areas. A perfect reflector would generate a reflectance of 1.0 at any given wavelength.

(UVA, 320–400 nm) radiation is thought to enhance target contrast (e.g. Browman, Novales-Flamarique & Hawryshyn 1994, and see Discussion in Johnsen & Widder 2001). Thus, the UVA reflection pattern of salmon (Fig. 1) may also improve host location/settlement, if the louse can perceive UVA radiation.

In the work reported here, we tested whether lighting conditions – including POL and UVA – affect the overall settlement, and/or location of settlement, of infective stage *L. salmonis* (copepodids) on salmon in experimental tanks.

Materials and methods

Collection of *Lepeophtheirus salmonis*

Adult *L. salmonis* with egg strings were collected from live salmon maintained in sea cages, or from salmon at the slaughterhouse. Adult lice were transported to the laboratory where egg strings were separated from the female using a scalpel. Detached egg strings were placed in a hatching container (a 100 μm sieve of 50 cm diameter) suspended in a running water bath at 8 °C and under a 24 h light photoperiod. Sieves were checked daily for the presence of hatched nauplii. If any nauplii were present, the contents of the sieve were gently washed down into a white bowl. Unhatched egg strings were transferred back to the sieve, which was resuspended in the water bath after being cleaned of residue. Nauplii were then transferred into another container (a 100 μm sieve of 25 cm diameter) for on-growing in a water bath at the same temperature.

Salmon for infection studies

Atlantic salmon (NLA strain) were used for infection studies. To eliminate the possibility that any settlement of *L. salmonis* could have occurred in the sea, salmon were maintained in land-based tanks after transfer from the hatchery. Thus, none of the salmon had been subject to infections with salmon lice prior to these experiments. In each experiment, all the salmon were of the same age group. In the first experiment, 11–15 salmon of similar size (736.6 ± 27.7 g) were placed into each tank. In the second experiment, the salmon available were smaller (125.5 ± 1.2 g). Thus, 18–21 fish were placed into each tank so that a similar fish body surface area was available in both experiments. Experiments conducted in an analogous manner by Glover, Hamre, Skaala & Nilsen (2004), concluded that normalizing lice abundance by fish surface area is a suitable method of removing fish size bias among groups challenged with lice. Thus, despite the difference in fish size, we could still compare settlement in our two experiments.

Infection protocol

The infection protocol used in these experiments conforms to that used in other studies of settlement by *L. salmonis* (Glover *et al.* 2004 and references cited therein). Round tanks (1.5 m diameter, filled with 1582 L of water) were chosen to avoid the possibility of still water refuges forming in corners where copepodids could aggregate. Salmon were allowed at least 2 days to acclimatize (at 8 °C) in the tanks before beginning the infection experiment. The water supply (30 L min^{-1}) was turned off 5 min before introducing infective-stage *L. salmonis* copepodids. During this time, the water level in the tank was lowered to 1/3 that of full volume and the water inflow was shut off. Even at this reduced water level, there remained enough room for the salmon to swim normally and there was no significant depletion in oxygen concentration. A single copepodid group that was large enough to infect all the tanks in the experiment was chosen from the on-growing system described above. This assured that all the lice were of similar age (copepodid day 3) and developmental state. The copepodid population was subsampled, counted, and the per volume density of animals was calculated. In both the experiments, 600 infective-stage copepodids were introduced into each of the experimental infection tanks while the water level was 1/3 full (with no water flow). After 90 min, the water flow was turned back on and the tank volume was returned to its full level. At the flow rates used, the water in the test tanks would have been replaced every 53 min. Thus, copepodids that had not already settled onto a salmon after the 90-min infection period would have been flushed out of the tank within a few hours at most.

Light treatments

In a first experiment, settlement was evaluated under three lighting conditions; L1: unpolarized under UVA-through visible; L2: unpolarized without UVA (control); L3: 100% linearly polarized

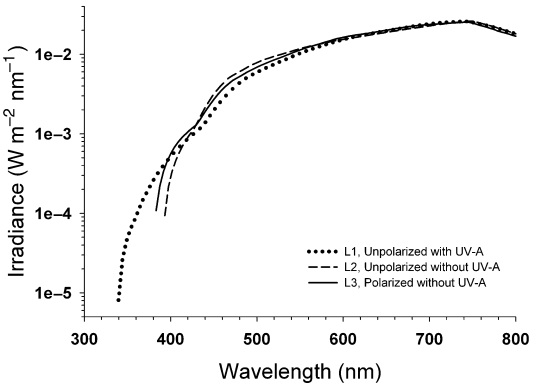

Figure 2 Spectral irradiance of the light treatment groups (L1, L2 and L3) under which *Lepeophtheirus salmonis* settlement on Atlantic salmon was tested. The photon fluxes (L1–L3) were $1.92 \times e^{19}$ photons m^{-2} s^{-1} for unpolarized with UVA; $1.90 \times e^{19}$ photons m^{-2} s^{-1} for unpolarized without UVA; and $1.99 \times e^{19}$ photons m^{-2} s^{-1} for polarized without UVA.

without UVA (Fig. 2). These lighting and spectral conditions were obtained using standard 500 W halogen lamps positioned directly above the centre of the tanks. L1 tanks were covered with 'Tech Spec' linear polarizing film sheet (Edmund Industrial Optics Ltd, NY, USA catalog# P45-204). L2 tanks were covered with a UV-blocking clear plexiglass sheet (Röhm GmbH, Darmstadt, Germany; catalog# GS-231, 3 mm thick). L3 tanks were not covered. There was no UV-polarized light treatment because of the difficulty in obtaining large sheets of UV-transmissive polarizing material. To ensure that all treatments received the same photon flux, lamp outputs were measured from 280 to 800 nm with an Optronic Laboratories (Orlando, FL, USA) OL754 scanning spectrophotometer. The current to the lamps was then adjusted accordingly, within the range that did not affect their spectral output (Fig. 2). There were two replicate tanks per light treatment, for a total of six tanks. The photon fluxes in treatments L1–L3 were $1.92 \times e^{19}$, $1.90 \times e^{19}$ and $1.99 \times e^{19}$ photons m^{-2} s^{-1}, respectively.

In a second experiment, settlement was evaluated in the dark. Two tanks were surrounded with opaque material (several layers of black plastic) and the room lights were kept off during the entire experiment. As a control for this experiment, a single-tank parallel was conducted under unpolarized white light, without UVA (under standard fluorescent tubes).

Spectral reflectance

The spectral reflectance (280–800 nm) from various regions of the salmon body surface was measured using an Optronic Laboratories IS-1000 integrating sphere, coupled to the OL-754 scanning spectrophotometer. The IS-1000 compares the reflectance of any surface to that of a Teflon standard (which is a perfect reflector, i.e. with a reflectance of 1.0). Salmon were anaesthetized with a benzocaine solution and, immediately after the fish stopped moving, reflectance was measured at three locations, ventral (along the lateral line groove between the pectoral and pelvic fins), dorsal (in front of the dorsal fin) and the caudal area.

Evaluation of *Lepeophtheirus salmonis* infection

Infection levels on fish were evaluated 20 days after the start of the experiments, when the animals undertook ecdysis from chalimus II to chalimus III. This was to ensure that the animals were large enough to be seen on the body surface of the fish. As we are not aware of any evidence to the contrary, we assumed that there was no significant change in the parasite's position on the body surface during the 20 days from settlement to censusing.

The water level in the tanks was lowered to approximately twice the fish's body depth and 40 mL of a benzocaine solution (500 mg benzocaine L^{-1} ethanol) was added to mildly anaesthetize the salmon. This was undertaken so that fish could be examined for infection without them thrashing about, thus preventing the possibility of salmon lice falling off. The salmon were then netted and placed into tubs containing enough benzocaine to anaesthetize, but not kill them. The number of *L. salmonis* on each fish, and their locations on different sections of the body surface, were recorded. Body surface sectors were modified from Jaworski & Holm (1992) and were as follows (numbers in parentheses correspond to the percentage of the total body surface area represented by this region): (a) head: the frontal region of the fish, back to the most caudal end of the operculum (11%); (b) dorsal: the dorsal sides, including the dorsal and adipose fins down to the lateral line groove (20%); (c) ventral: the ventral sides, up to the lateral line groove, including the fins (60%); (d) tail: the tail and the area delimited by the line from the edge of the fin rim on the dorsal side to the edge of the fin rim on the ventral side (9%). After the lice

were counted, the fish were revived in running water. There were no mortalities.

Results

Spectral reflectance from the body surface of the salmon used in these experiments was low (2–3%) in the dorsal and caudal regions, but high (up to 83%) and spectrally broad in the ventral region (Fig. 1).

The total number of *L. salmonis* settling on fish in experiment 1 ranged from 143–249 per tank/replicate, representing an infection rate of 24–42% (Table 1). The mean number of lice settled per fish ranged from 15 to 18 (Table 1). No statistically significant difference (Kruskal–Wallis ANOVA, $P = 0.524$) was found in total louse settlement between the three (L1, L2 and L3) light treatments (Fig. 3a). In all treatment groups there was a preference for the dorsal and ventral positions over the head and tail (Kruskal–Wallis ANOVA, $P < 0.001$, Dunn's pairwise multiple comparison, $P < 0.05$). For each fish the average number of lice settled on the head and tail was approximately one, and the numbers of lice settled on the dorsal and ventral sides was approximately seven (Fig. 3a).

In the second experiment, the total number of lice settled ranged from 113 to 160 per tank, which corresponds to an infection rate of 19–27% (Table 1). The mean number of lice settled on each fish ranged from five to eight (Table 1). There was no statistically significant difference between total lice settlement in dark vs. light treatment groups (ANOVA, $P = 0.672$). As in experiment 1, there was a preference for the dorsal and ventral position over the head and tail (Kruskal–Wallis ANOVA, $P < 0.001$, Dunn's pairwise multiple comparison, $P < 0.05$, Fig. 3b). The average number of lice on the head and tail was approximately one, and on the dorsal and ventral sides, approximately three.

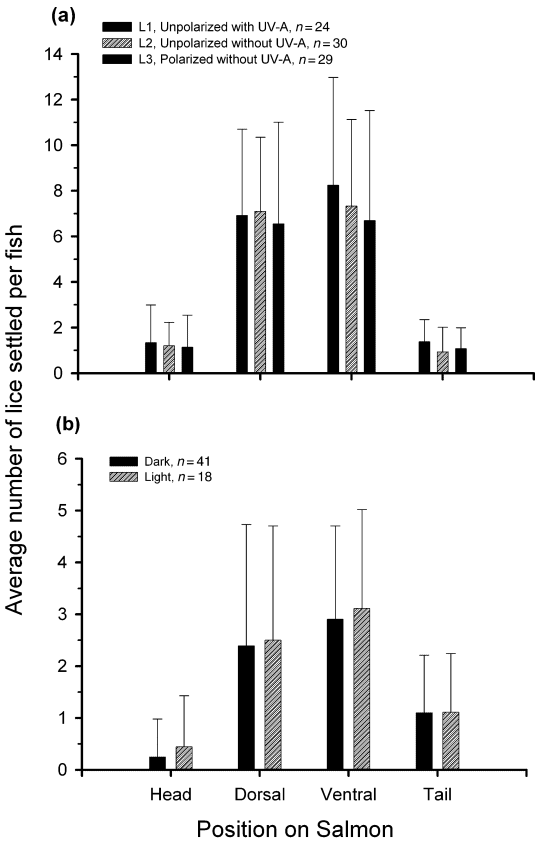

Figure 3 (a) Mean (± SD) number of *Lepeophtheirus salmonis* settled on different body regions of Atlantic salmon in each light treatment group (L1, L2 and L3). (b) Mean (±SD) number of lice settled under dark vs. unpolarized white light (without UVA) conditions. *n* is the total number of fish in each treatment group.

The difference in the rate of settlement between these two experiments is consistent with the variability in such data as observed in other studies

Table 1 Number of Atlantic salmon used in each experimental tank, total number of *Lepeophtheirus salmonis* copepodids which settled on the fish, the average number settled per fish, and percent settlement

Treatment	Number of fish	Total no. of lice settled (of 600)	Mean no. of lice settled per fish (SD)	Settlement (%)
Experiment 1				
L1 (replicate 1)	11	192	17.5 (8.4)	32
L1 (replicate 2)	13	237	18.2 (10.7)	40
L2 (replicate 1)	15	249	16.6 (6.0)	42
L2 (replicate 2)	15	159	16.5 (3.2)	27
L3 (replicate 1)	14	227	16.2 (8.4)	38
L3 (replicate 2)	15	143	14.7 (9.6)	24
Experiment 2				
Dark 1	21	113	5.4 (2.4)	19
Dark 2	20	160	8.0 (5.4)	27
Light	18	129	7.2 (4.0)	22

of this nature (Glover *et al.* 2004 and references cited therein).

Discussion

The importance of light in the settlement ecology of *L. salmonis* is highlighted by the field-oriented results of Hevrøy *et al.* (2003) and by experimental work on the swimming responses of lice to changes in light intensity (Novales Flamarique *et al.* 2000). Thus, if UVA, POL, or light in general were important in the proximity stages of the host location and settlement process, then there should have been more lice on the fish in those treatments, and/or their settlement locations should have been different; this was not the case.

There was a consistent preference for settlement onto the dorsal and ventral areas of the body in our study, as in the earlier work of Bron, Sommerville, Jones & Rae (1991). These settlement location preferences are not clearly related to regions of the body surface exhibiting different spectral reflectance (see Fig. 1). Microenvironment selection of *Gyrodactylus derjavini* on the body surface of rainbow trout, *Oncorhynchus mykiss* (Walbaum), is apparently related to the presence and density of superficial mucous cells (Buchmann & Bresciani 1998). Unfortunately, the mucous cell distribution in salmon is not known. Thus, until additional information becomes available, the most parsimonious explanation for our observations is that these sites were 'preferred' only passively, as the larger relative surface area of these regions represents a bigger target for settlement.

The lack of enhanced settlement (or differences in settlement location) under different lighting conditions might be attributed to (a) the absence of a discrete UVA and/or POL receptor channel in this species (see Discussion in Novales Flamarique *et al.* 2000) or (b) the presence of a UVA and/or POL receptor channel that is utilized for something other than object and pattern recognition, or target contrast enhancement (see Cronin *et al.* 2003), (c) a coupled POL/UV channel, as is the case for crabs (Cronin & Forward 1988), stomatopods (mantis shrimps) (Marshall, Cronin, Shashar & Land 1999) and damselfish (Hawryshyn, Moyer, Allison, Haimberger & McFarland 2003) or (d) an artifact of the small tank systems in which these experiments were conducted; at such close proximity the louse may rely upon olfactory and mechano-sensory modalities of host detection rather than vision. A rigorous assessment of spectral and POL sensitivity in the louse is required to discriminate amongst the possibilities (a) vs. (b) vs. (c).

The sensory modalities and behaviours involved in host detection and recognition by *L. salmonis* consists of a spatio-temporal hierarchy within which one or more senses operate simultaneously. Visual cues, such as decreases in light intensity resulting from shadows cast down into the water column by fish swimming overhead would operate at long range – metres to tens of metres. Such signals alter the parasite's overall activity level and/or swim pattern, typically motivating it to move toward the source (Novales Flamarique *et al.* 2000; Mikheev *et al.* 2003). *Lepeophtheirus salmonis* is, in fact, very sensitive to decreases in light intensity (Novales Flamarique *et al.* 2000). Increases in light intensity, such as flashes off the side of a fish, can also sometimes induce directed swimming behaviour, as is the case for the fish ectoparasite *Argulus foliaceus* (e.g. Mikheev *et al.* 2003). Light flashes would probably be visible over shorter distances than shadows. Diffuse chemical cues, such as the 'smell' of a large group of salmon on a migratory run or in sea cages, may also act as directional cues over scales of metres to tens of metres, and they would persist longer than a shadow or a light flash. A diffuse, host-related chemical cue could also alter the louse response to visual cues, as is the case for *Argulus coregoni*, which located hosts more effectively using vision when olfactory cues were present (Mikheev *et al.* 2004). Thus, shadows, light flashes and diffuse chemical cues would all attract a population of free-swimming lice towards a population of potential host fish over fairly long spatial scales. However, the chemical trails that might be associated with a single fish operate on small spatio-temporal scales – perhaps only a few cm (e.g. Okubo, Armstrong & Yen 2001; Ingvarsdóttir *et al.* 2002a,b). For most copepods, hydrodynamic cues are also only effective on scales of mm to a maximum of 3–4 cm, and they are fleeting (e.g. Doall, Strickler, Fields & Yen 2002; Yen & Okubo 2002). This also appears to be true for salmon lice copepodids, which responded to a moving plaster cast of a salmon head over maximal distances of 3–4 cm (Heuch & Karlsen 1997; P. A. Heuch, unpublished results and personal communication). Finally, at settlement, chemical and tactile cues associated with the surface of the host are probably most important (e.g. Buchmann & Bresciani 1998). Thus, over smaller spatio-temporal scales, such as in

our experimental tanks, where vision is unimportant to *L. salmonis*, it is probable that the parasite relies on olfactory and mechano-sensory cues to locate salmon. Similar results were found by Mikheev *et al.* (2003): settlement of *A. foliaceus* on its host fish was actually higher in the dark than in the light. Mikheev *et al.* go on to describe a hierarchy of host search behaviour for *A. foliaceus* which is analogous to that discussed above. Additional research on the responses of *L. salmonis* to various host-related cues, under a variety of experimental conditions and at different spatial and temporal scales, is required to fully resolve their host-finding behaviour.

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