Detection of infrasonic water oscillations by copepodids of *Lepeophtheirus salmonis* (Copepoda: Caligida)

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**Abstract.** The cues that trigger infection of fish by parasitic copepods are largely unknown. We show that copepodids of the parasitic copepod *Lepeophtheirus salmonis* respond to uniform, linear accelerations, which are similar to those found in front of a swimming fish. Copepodid responses to vibrations at 1, 3, 5 and 10 Hz frequency were filmed and analysed. The animals were stimulated in a completely water-filled, clear perspex chamber, which was suspended like a swing in four wires from a steel frame. The chamber was moved by a vibrator which was fed amplified signals from a sine wave oscillator. On stimulation, copepodids responded by executing swimming bursts of 1-3 s duration. There was no apparent preferred swimming direction. Sensitivity was highest at 3 Hz, with a threshold value of $5 \times 10^{-3}$ m s$^{-2}$ (rms). At 1 Hz the threshold was <6 dB higher, and sensitivity was markedly reduced at 10 Hz, where the threshold was $1.8 \times 10^{-1}$ m s$^{-2}$ rms. These results indicate that the copepodids may react to the near-field accelerations produced within centimetres of a swimming fish. Acceleration sensitivity may therefore be a cue that triggers high-speed swimming and subsequent infestation of the host. If this ability is present in holoplanktonic copepods, it may facilitate detection and escape from predatory fish.

**Introduction**

Numerous studies have reported that copepods may change their behaviour in response to local water disturbances. The most common response is avoidance or abrupt escape (e.g. Strickler, 1975; Swift and Fedorenko, 1975), but attacks on 'prey' may also be elicited (Schröder, 1967; Landry, 1980; Bailey and Yen, 1983; Jonsson and Tiselius, 1990). In most behavioural studies examining the mechanoreceptive abilities of copepods, the hydrodynamic stimuli given to the animals have been poorly defined. The precise nature of water movements acting as stimuli, and the thresholds and frequency sensitivity of the mechanoreceptive structures have thus remained largely unknown. However, some carefully designed behavioural and electrophysical studies have been conducted to address these questions.

*Calanus finmarchicus* carried in a current towards a stationary rod have been shown to dart off just before they reach the obstacle (Haury *et al.*, 1980). The authors concluded that the amount and rate of fluid deformation (e.g. shear) in the immediate vicinity of the animal were the effective stimuli for the avoidance reaction. This copepod did not respond to uniform water acceleration even at high intensities (Haury *et al.*, 1980). In contrast, the best predictor of escape of *Acartia hudsonica* nauplii from the feeding current of a *Temora longicornis* seemed to be its relative velocity (Yen and Fields, 1992). This would indicate that...
inertial mechanisms are of relevance for *A. hudsonica* nauplii. As the animal is slightly denser than the surrounding water, its body will lag behind, but the appendages will follow when the water is accelerated. A negative rheotactic response to acceleration of the surrounding water has been demonstrated in the freshwater copepod *Cyclops abyssorum* (Schröder, 1967). Furthermore, this species seemed to lose orientation and responsiveness when accelerated in a medium with the same density as its own. A loss of orientation in water modified to eliminate density differences has also been observed in *Cyclops scutifer* (Strickler and Bal, 1973). This led Strickler and Bal (1973) to suggest that holopelagic copepods may sense the net force of different acceleration of the surrounding water and their own body. The authors reasoned that this could function both as an orienting stimulus and a predator detection mechanism. However, the density difference between copepods and water is small, and they are therefore generally not expected to detect water vibrations in a manner comparable to teleosts using their otolith organs (Hawkins and Myrberg, 1983).

A substantial proportion of the known copepod species are parasitic, and they are found in half of the copepod orders (Huys and Boxshall, 1991). The infective stages of these must not only avoid being eaten by a potential host, but also be able to respond to the presence of a host, and swim to infest it. Hosts of parasitic copepods unintentionally produce a variety of stimuli which may signal their presence to the parasites. Chemical, light-related and mechanical information have been implicated in the infestation process. Fish excrete chemical substances, such as mucus and bile salts, that may be specific to their species. (Døving, 1989). If the fish host is stationary, it may produce chemicals for a long enough period of time to create an odour gradient with gradually decreasing concentration of active substance away from itself. Parasites may in such a case migrate up the gradient to the source. Several authors have described the attraction of the infective stage, the copepodid, to substances produced by the host (Fasten, 1913; Carton, 1968a,b; Fraile, 1989). For the salmon louse, *Lepeophtheirus salmonis*, no attraction of the copepodids to any host-derived substances has been recorded (Bron et al., 1993; personal observation). This may indicate that the rapidly swimming, solitary salmonid does not provide a reliable chemical cue for host-finding. Passing shadows may also signal the host’s arrival to an infective copepodid. Shadow responses have been reported for copepodids of the genus *Salmincola* (Fasten, 1913; Kabata and Cousens, 1977; Poulin et al., 1990; Conley and Curtis, 1993), but not for *L. salmonis* (Bron et al., 1993). Actual infestation by shadow response has, however, never been demonstrated.

Even though chemical and light-related cues cannot be eliminated, mechanical stimuli seem the most probable host-related factor to induce settling by salmon louse copepodids. In *Salmincola edwardsii*, *Salmincola californiensis*, and *L. salmonis*, water movement induces higher activity levels (Fasten, 1913; Kabata and Cousens, 1977; Poulin et al., 1990; Conley and Curtis, 1993). In the laboratory, *L. salmonis* copepodids seem to display a spiralling or looping behaviour in response to strongly directional water currents (Bron et al., 1993). The reaction patterns of the copepodids are more likely a response to differential (shear) or uniform water accelerations than specifically to water jets. If copepod species
parasitic on fish have the ability to detect the water accelerations formed in front of swimming fish hosts (Kalmijn, 1989), it would give them a maximum amount of time to detect the fish and swim to infest it.

A fish swimming through the water produces near field movements, which are movements of mass, and a vibration of water molecules around their position, which is known as far field sound. The latter movements are very small, and at low frequencies, they are negligible compared to the local flow near the moving object (Kalmijn, 1988). Kalmijn (1988) and Enger et al. (1989) reported that the frequency components produced by a goldfish approaching and passing the displacement detector, were mainly below 20 Hz. Similarly, Bleckman et al. (1991) found that moving fish mainly produced water accelerations below 10 Hz. Twenty herz is the upper limit of the infrasonic range, which is defined as frequencies lower than can be detected by the human ear. Near and far field components are equal at a distance of half the wavelength away from the sound source. This occurs 75 m from the source at 10 Hz, and further off at lower frequencies. In front of a moving fish, then, near field water movements will dominate completely.

In this paper we test the hypothesis that a part of the flow field, the uniform accelerations below 10 Hz, triggers swimming activity that would bring the copepodid to its host. The response of *L. salmonis* copepodids to accelerations of different intensities and frequencies was recorded.

Copepodids responded with a strong rise in activity to the frequencies tested. This is the first time infrasound sensitivity has been documented for any copepod, and we suggest such a sensory ability may be important for both host- and predator detection in other copepod species.

**Method**

**Study animal**

*Lepeophtheirus salmonis* is a parasite of salmonids, with a circumpolar distribution in the northern hemisphere (Kabata, 1979). By grazing on mucus and skin it causes osmotic stress and secondary infections, and is therefore a serious pest in marine salmoniculture in the North Atlantic (Stuart, 1990; Costello, 1993). It has ten stages, including two nauplius (planktonic), one copepodid (planktonic, infective stage), four chalimus (fixed to host), two preadult (mobile on host) and the mobile adult stage (Johnson and Albright, 1991). For the present work we reared copepodids as described by Heuch et al. (1995) and Heuch (1995). The animals, which were 1–6 days old, were transported from the University of Oslo to the Biological Station at Drøbak (30 km), where the experiments were carried out. They were allowed to acclimatize for at least 2 h in the experimental chamber before stimulation began. Fresh animals were used every day.

**Experimental set-up**

The apparatus used has been described in detail by Karlsen (1992). Briefly, it consisted of a transparent perspex chamber suspended from a steel frame in four 40
cm steel wires like a swing. Background noise was reduced by fixing the frame to a steel plate attached to a 100 kg concrete block resting on 15 cm of dry sand poured on the concrete floor. The chamber was driven by a vibrator with a 10 mm working range, which was fed sine waves by a waveform generator. The displacements of the chamber were measured by a linear variable differential transformer (LVDT). The velocity and acceleration of the chamber were calculated from the displacements. The chamber was circulated with filtered 10°C, 30% S sea water at ~10 ml min⁻¹. Animals were added through an opening in the top, which was closed by locking screws before the chamber was completely filled with water. Light was provided by a neon tube covered by white perspex, which was placed behind the chamber. The animals gathered near the side which was closest to the light. A Hitachi Hi8 video camera was placed on the opposite side, and the copepods were clearly visible as dark objects against the light background. The focal plane was fixed a few millimetres from the side wall to ensure that responses of copepodids touching the wall or its boundary layer were not recorded. Most movements were at right angles to the view of the camera. One minute of background activity was recorded before and after each stimulation, between which there were at least 5 min.

**Video and data analysis**

Tapes were replayed frame by frame (25 frames s⁻¹) on a computer screen using Apple's Video Monitor program. This has a transparency mode of video display, which allowed images to be seen through an image analysis program window. We used NIH Image version 1.59 software to trace copepodid swimming patterns. For each stimulation, all movements of the copepodids within a 450 × 450 pixel window were traced with a ‘pencil tool’. Animals swimming into the window were ignored, if they had not started in the window and swam back into it. Usually, between 15 and 50 copepodids were present within the window at any one time. Their movements were traced for 1 s from stimulus onset. Traces were then reduced to one pixel width, and the number of pixels traced was counted for each stimulus. The total swimming distance of all copepodids in 1 s, divided by the number of copepodids within the 450 × 450 pixel window gave a direct measurement of copepodid activity. Calibration was done by filming a millimetre ruler.

Vibration thresholds were determined in the following way. First, a background level of activity (in terms of distance covered per copepodid) was estimated by averaging activity from 50 randomly selected, 1-s periods from each day. These values were found to be log-normally distributed. Second, the standard deviation for the background was estimated from the pooled values for 4 days to increase precision. This could be done as log-normally distributed populations have a constant coefficient of variation (CV = SD/mean). Third, the threshold level for a response was set to 95% of the background activity values that day by using a table of proportions of the normal curve. This corresponds to accepting an average activity of more than \( e^{(1.65SD + \text{mean of background activity})} \) pixels as a response. Fourth, both responses and non-responses from each frequency were
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fitted to a logistic regression model with intensity of stimulation (in terms of rms amplitude acceleration) as the predictor variable. The intensity that gave a 50% probability of response was then estimated for each frequency by inverse prediction.

Linear regression was only employed if response variables as well as residuals were found to be normal by the Shapiro-Wilks W test.

**Results**

Background activity was estimated for each day of experiment by recording average activity (distance covered) in 50 randomly distributed 1-s periods (Figure 1A). The natural logarithms of the background values were found to be normally distributed by the Shapiro-Wilks W test. Pooled values for all days (*n* = 400) showed that the copepodids covered 1.55 (± 0.17 SD) mm s⁻¹ on average when the system was undisturbed.

The copepodids reacted to the movements of the experimental chamber by increasing their average swimming activity (Figure 1B). The stimulus duration was 2–4 s. A typical response lasted 1–3 s, the activity always returned to background level within 5 s of stimulus onset (Figure 2). Usually, the average distance covered during a response far exceeded the background activity level. In the responses, 26–47% (mean 42 ± 12% SD, *n* = 46) of the animals swam longer than 95% of the background average swimming distance. This means that for the response shown in Figure 2, the 42% covered an average of ~17 mm/0.42 = 40 mm in the 3 s after stimulus onset. Between the responding copepodids there were large variations in swimming distance (cf. Figure 1B). Frequently some individuals swam 9 cm or more during the first second after stimulus onset.

Vibration thresholds for *L. salmonis* copepodids were determined by logistic regression of responses and non-responses to 147 stimuli. The intensity of stimulation (in terms of rms acceleration) that gave a 50% probability of response

![Fig. 1. Typical image of the swimming activity of *L. salmonis* copepodids recorded when they were: (A) not stimulated and (B) stimulated by 9.4 × 10⁻³ m s⁻² (rms) sound at 3 Hz.](https://academic.oup.com/plankt/article-abstract/19/6/735/1521406/739)
was estimated for each frequency (Figure 3). The fit of the logistic models was significant, with $P < 0.006$ for all frequencies. The copepodids were most sensitive to 3 Hz sound, with a threshold intensity of $5.1 \times 10^{-3}$ m s$^{-2}$. However, at 1 Hz the sensitivity was reduced by $<6$ dB, and at 5 Hz it was slightly more than 6 dB down. At 10 Hz, the intensity giving a 50% probability of response was more than an order of magnitude higher than at 3 Hz.

**Fig. 2.** A typical average response of *L. salmonis* copepodids when stimulated with $1.1 \times 10^{-2}$ m s$^{-2}$ (rms) sound at 3 Hz. Line indicates no stimulus, box indicates stimulus.

**Fig. 3.** Sensory thresholds of *L. salmonis* copepodids in the frequency range 1–10 Hz, as estimated by inverse prediction based on logistic regression of 147 positive and negative responses. The intensity of stimulation (in terms of rms acceleration) that gave a 50% probability of response ($\pm$ SE) is presented for each frequency.
At 1, 3 and 5 Hz, the average distance covered by the copepods increased significantly as intensity of stimulation increased from threshold in steps of 6 dB (Kruskal-Wallis test, $\chi^2$ approximation, $P = 0.022$ for 1 Hz, $P = 0.0057$ for 3 Hz, $P = 0.034$ for 5 Hz, Figure 4). The 5 Hz dataset, which included more values than shown, was analysed by linear regression with intensity (rms acceleration) as the predicting variable. This procedure showed that acceleration can explain 55% of the variations in the mean distance (exceeding the average background) covered by the copepods ($F$ ratio $= 33.1581$, $P < 0.005$). At 10 Hz, there was no significant difference in activity at the intensities shown (Figure 4, Kruskal-Wallis, test, $\chi^2$ approximation, $P = 0.34$).

The increasing activity at increasing intensity at 1, 3 and 5 Hz could either be caused by a larger number of animals responding, or by the reacting copepods swimming faster. Copepods that did not react to the sound stimulus either just
sank or swam very short paths. Their contribution to the total distance covered was very small. The path length of reacting animals in the responses could therefore be estimated by dividing the total distance covered (number of millimetres swum by all copepodids in the window), by the number actually responding (Table I). At 5 Hz, this mean distance did not differ significantly between intensities (Kruskal-Wallis test, $\chi^2$ approximation, $P = 0.10$), but the mean percentage of animals responding was significantly different (Kruskal-Wallis test, $\chi^2$ approximation, $P = 0.009$). Thus the increase in average activity at higher intensities was due to a higher number of animals responding to the stimulus. Statistical inference from the two other frequencies was difficult since sample sizes were too small.

The copepodids were tested for habituation to a 3 Hz, 0.024 m s$^{-2}$ stimulus delivered at 10 s and 1 min intervals (Figure 5). A linear regression of responses on time showed that response strength (mean distance covered s$^{-1}$) did not diminish when stimuli were administered at the longer interval ($r^2 < 0.005$, $P = 0.99$). However, a 10-s interval between stimuli appeared to reduce the response slightly ($r^2 = 0.24$, $P = 0.0499$, slope: $-0.95 \pm 0.44$ SE).

**Discussion**

The present study provides the first evidence that the copepodids of *L. salmonis* can detect uniform water accelerations in the infrasonic range. It is also the first report of infrasonic acceleration thresholds of a copepod measured under controlled conditions. We found that increasing intensity induced more animals to respond, and that response strength diminished when stimuli were delivered at very short intervals. The results obtained are compared with mechanosensory abilities described in holoplanktonic copepods, and discussed in the context of host finding.

The experimental set-up used effectively simulated infrasonic water displacements (Karlsen, 1992). The horizontal oscillations of the experimental chamber exceeded the vertical movements by >30 dB. At stimulus intensities of $10^{-3}$-$10^{-1}$ m s$^{-2}$, the pressure variations within the chamber were ~0.11–10 Pa rms (Karlsen, 1992), which are orders of magnitude below the pressure sensitivity that was found in *C. finmarchicus* (Rice, 1962) and in *L. salmonis* (Bron et al., 1993). Pressure itself was therefore most likely not responsible for the observed responses.

**Table I.** Parameters characterizing the responses (i.e. where the distance covered per animal per second exceeded 95% of the background values) of *L. salmonis* copepodids to 1, 3 and 5 Hz sound at different intensities

<table>
<thead>
<tr>
<th></th>
<th>1 Hz</th>
<th>3 Hz</th>
<th>5 Hz</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Acceleration (m s$^{-2}$ rms)</strong></td>
<td>0.009</td>
<td>0.017</td>
<td>0.008</td>
</tr>
<tr>
<td><strong>Number of responses</strong></td>
<td>6</td>
<td>10</td>
<td>6</td>
</tr>
<tr>
<td><strong>Mean % of copepodids reacting (SD)</strong></td>
<td>46.0 (6.2)</td>
<td>46.6 (13.0)</td>
<td>33.4 (8.8)</td>
</tr>
<tr>
<td><strong>Mean distance covered by reacting copepodids (mm) (SD)</strong></td>
<td>13.6 (1.8)</td>
<td>14.3 (4.2)</td>
<td>14.7 (4.7)</td>
</tr>
</tbody>
</table>
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In the present study. The flow rate through the chamber was small, and the stimulus oscillations did not seem to alter the flow pattern significantly. Furthermore, stimulus responses were not reduced when the flow was turned completely off. We were therefore confident that the copepodids responded to the horizontal accelerations of the surrounding water, as measured with the LVDT sensor.

**Comparison with the acceleration sensitivity of holoplanktonic copepods**

The thresholds obtained were \( \sim 5 \times 10^{-3} \text{ m s}^{-2} \) in the frequency range 1–3 Hz. At 10 Hz the sensitivity was clearly reduced compared to the lower frequencies. This suggests that the detection of uniform water flows in *L. salmonis* is limited to the infrasonic range. Habituation to the low frequency stimulus was not observed. The weak trend of smaller responses when the stimulus was delivered at 10-s intervals was more likely due to exhaustion. To our knowledge, acceleration sensitivity has previously only been examined in *Cyclops abyssorum* by Schröder (1967). The experimental design in his study was aimed at producing a negative d.c. acceleration over a distance of 20 cm, corresponding to a stimulus duration of \(~2\text{ s}\). Although the d.c. stimulus obviously was contaminated by unknown higher order frequency components, the main frequencies were still most likely below 10 Hz. The threshold for eliciting rheotaxic responses in *C. abyssorum* was \( 1.3 \times 10^{-3} \text{ m s}^{-2} \), which compares well with the thresholds obtained in *L. salmonis*. It should be noted that our method of threshold estimation is rather conservative, as both activity levels qualifying and not qualifying as a response were entered in the logistic regression model.

In the study of Yen and Fields (1992) the flow field above the first antennae of *Temora longicornis* was described in terms of velocity. When the flow field is recalculated in terms of acceleration, the values eliciting escape reactions range
from 1 to $5 \times 10^{-3}$ m s$^{-2}$, and the dominating frequency component(s) are probably well below 20 Hz. Thus, the uniform accelerations experienced by the *Acartia* nauplii entering the feeding current of *T.longicornis* may also have been a relevant stimulus parameter for escape reactions observed by Yen and Fields (1992). This suggestion is supported by the fact that *Acartia* sp. adults tested in our set-up responded to infrasonic vibrations with a sensitivity comparable to that of *L.salmonis* (H.E.Karlsen, unpublished observations).

**Sensory mechanisms**

Uniform hydrodynamic accelerations have been viewed as an unlikely source of mechanical information for copepods primarily because copepod density is so close to that of water. The animals are therefore generally expected to move with the same phase and amplitude as the surrounding water. This is clearly not true for all copepod species. The density difference between *Cabyssorum* and its test water was $\sim 0.022$ g cm$^{-3}$ (Schröder, 1967). The density of *L.salmonis* copepodids is 1.044 g cm$^{-3}$ (P.A.Heuch, unpublished data), whereas the sea water used in the experiments had a density of $\sim 1.023$ g cm$^{-3}$. Thus density differences of $-0.020$ g cm$^{-3}$ are sufficient to detect accelerations of $5 \times 10^{-3}$ m s$^{-2}$, corresponding to a displacement amplitude of $\sim 20$ μm at 3 Hz.

The antennulae of *L.salmonis* are each equipped with five long branched, three long smooth and three short smooth setae, and two aesthetascs (Gresty *et al.*, 1993). Compared to holoplanktonic copepods, the antennule of *L.salmonis* copepodids is rather short, $\sim 130$ μm, with the longest setae adding another 130 μm. However, the copepodid does not use its mouthparts or antennae to produce feeding currents, as is common among herbivore copepods. Consequently, in *L.salmonis* there is no need to keep the sensory elements far from the body to avoid masking and interference from feeding.

The mechanosensitivity of several copepod species has been investigated by stimulating the setae directly (Yen *et al.*, 1992) and with a vibrating sphere (Lenz and Yen, 1993). In these electrophysiological recordings it was shown that displacements of $10^{-8}$ m were capable of triggering spikes from the antennule of the copepods *Labidocera madura* (Yen *et al.*, 1992), *Euchaeta rimana* and *Pleuromamma xiphias* (Lenz and Yen, 1993). A water velocity of $2 \times 10^{-5}$ m s$^{-1}$ was required to produce spikes at high frequencies. This is a factor of 10 lower than for the *L.salmonis* copepodids in our experiments. However, our test frequencies did not extend beyond 10 Hz, whereas the above thresholds were obtained around 1000 Hz. The lowest thresholds in the above studies were obtained at frequencies close to 1 kHz and the sensitivity was greatly reduced at frequencies approaching 50 Hz. As pointed out by Yen *et al.* (1992), this is somewhat surprising since most biologically relevant underwater sounds and near field displacements are below 100 Hz (Newbury, 1972; Kirk, 1985; Kalmijn, 1988; Poulet and Gill, 1988; Bleckman *et al.*, 1991). Some crustaceans, such as spiny lobsters (e.g. *Palinurus* and *Panulirus*), and several fish species may produce sounds above 100 Hz (Hawkins and Myrberg, 1983), however, the relevance of these to copepods can be questioned. The identity of relevant underwater sources
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producing frequencies in the kilohertz range has yet to be clarified. One possible
source may be moving appendages on the copepods themselves (Giguère and

**Host detection**

The main concern for the infective stage of a parasitic copepod is evidently to find
and infect its host. During the searching it must also avoid predators. Copepodid
chemotaxis towards host-derived substances was demonstrated by Carton
(1968a,b) for the polychaete parasite *Sabelliphilus sarsi*, and Fraile (1989) for
*Caligus minimus*, which parasitizes sea bass *Dicentrarchus labrax*. However, Bron
et al. (1993) found no evidence of attraction to salmon tissue components by
*L. salmonis* copepodids, nor did they observe any response to passing shadows.
This leaves the near field water motions produced by the host as the most likely
stimulus for host detection in *L. salmonis*. Increased activity upon stimulation
with 'shock waves' was reported for copepodids of the parasitic copepod *Salmin-
cola edwardsii* (Poulin et al., 1990), indicating that mechanical stimuli are relevant
also in this species.

For an attacking copepodid, the anteriolateral flow field about a swimming host
fish is expected to be of highest significance. This field is essentially a low-
frequency hydrodynamic dipole field derived from water being pushed ahead of
and along the sides of the advancing fish (Kalmijn, 1988, 1989). In fact, Kalmijn
(1988) reported that the frequency components produced by a goldfish approach-
ning and passing the displacement detector, were mainly below 20 Hz. The fre-
quency range determined for *L. salmonis* thus seems to fit quite well to the flow
fields produced by an approaching host. A swimming fish will, in addition to
hydrodynamic local flows, also cause compressions and rarefactions of water, thus
propagating sound waves. However, in the inner near field, i.e. within metres
from the source at frequencies below 20 Hz, the fluid motions due to propagat-
ing waves are negligibly weak compared to hydrodynamic flows. The amplitude
of near field water displacements will strongly depend on the distance to and the
speed and volume of the source. If the acceleration fields above the threshold of
copepodids are within a few centimetres of the fish, the expected host detection
distance in *L. salmonis* would be comparable to its reaction distance as observed
in the present study. Further research in this field should include filming of the
actual infestation process with live fish as a target, and detailed studies of the
properties of flow fields of swimming host fish.

We conclude that uniform, near field accelerations produced by swimming
salmonids are likely to induce high-speed swimming and subsequent infestation
by salmon louse copepodids. However, this is but one component of the complex
flow field surrounding the fish. Rotational water movements will also contribute
to the total sensory input of the copepodid, possibly working in synergy with the
uniform movements. For holoplanktonic copepods, sensitivity to both types of
water movements might enlarge the perceptive range, and thus give more time
to escape from predatory fish.
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