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Gone with the flow: current velocities mediate parasitic infestation of an aquatic host

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ABSTRACT

Host–parasite interactions are moderated by the environmental conditions of the interaction medium (e.g. air or water). Encounter rate and the time available for a parasite to make physical contact with a host are both influenced by fluid dynamics, yet how they interact is poorly known. Here, we tested whether current velocities altered the initial attachment and post-settlement survival of an ecto-parasitic copepod (*Lepeophtheirus salmonis*) on Atlantic salmon. Current velocities strongly influenced attachment; infestation levels were 2.5 and 1.3 times higher in moderate than high and low velocity currents, respectively, while current velocities did not affect post-settlement survival. An interplay between a reduced host–parasite encounter rate in a low velocity current and reduced contact time in a high velocity current likely explains this result. Initial parasite attachment position was influenced by an interaction between current velocity and swimming behaviour, likely due to different fin positioning by fish in flows of different velocities. Our results imply that rapid swimming by salmon migrating out of coastal waters, usually described as adaptive against predation, could also be adaptive against parasitism. Infestation rates were also highest at the typical swimming speed of farmed salmon in coastal fish farms, which may be a hitherto unrecognised factor contributing to *L. salmonis* epidemics.

1. Introduction

Spatial and temporal interactions between hosts and parasites are crucial for the occurrence of disease. The fluid dynamics of the surrounding medium where hosts and parasites are present (i.e. air or water) frequently influence the occurrence of disease through their influence on dispersal, transmission and encounter rates between organisms. Aerodynamics mediate exposure rates to airborne disease-causing agents in medical facilities (Clark and De Calcina-Goff, 2009), and animal production systems (Tsukamoto et al., 2007). Airflow engineering of surgical theatres and ventilation arrangements in animal husbandry facilities are crucial in preventing airborne pathogens. In aquatic systems, flow hydrodynamics likely play a key role in host–parasite interactions (Peters, 2000), and could be a critical factor in the incidence of disease.

Flow hydrodynamics modify both the encounter rate and contact time between organisms in aquatic environments. Field and laboratory experiments in flume tanks, as well as mathematical models, show that water motion affects larval settlement of benthic marine animals (Koehl, 2007); rapid flows increase the encounter rate with surfaces, increasing larval settlement. Further, increased water turbulence is positively correlated with the incidence of parasitic diseases in planktonic algae caused by fungal parasites, which is thought to be due to higher encounter rates between hosts and parasites (Doggett and Porter, 1996). However, turbulence has been linked to a higher encounter rate up until a certain turbulence threshold, beyond which infection levels decrease due to reduced contact time (Kühn and Hofmann, 1999). This evidence suggests that fluid dynamics can be critical in determining the incidence of diseases in aquatic systems, but studies on marine host–parasite models are scarce.

Marine ecosystems are both qualitatively and quantitatively different from terrestrial environments, and these differences affect the application of models and management approaches to disease that have been developed for terrestrial systems (Ferguson et al., 2001; McCallum et al., 2004). Recent and rapid domestication of marine animals by industrial aquaculture has introduced billions of new hosts in high density settings into aquatic ecosystems (Duarte et al., 2007). As farmed and wild animals

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most often share the same water, the context of host–parasite interactions has been fundamentally altered for both. In marine ecosystems, salmon are the most frequently farmed fish. In these species, a highly important disease-causing agent, external parasitic sea lice (Costello, 2009a,b), cause substantial losses in farmed salmon (Costello, 2009a) and threatens wild salmon populations due to farm-induced amplification of parasite levels (Costello, 2009b; Krkošek et al., 2011, 2013). Salmon farms are flow-through systems connected to external influences (e.g. water salinity, temperature), which are critical in modifying sea louse infestation rates (Heuch et al., 1995; Tucker et al., 2000; Bricknell et al., 2006). Further, evidence suggests that current velocities are negatively correlated with sea lice levels on salmon (Revie et al., 2003), yet how flow hydrodynamics relate to infestation rates is poorly understood. No study has yet tested the effects of current velocities on sea louse initial attachment or post-settlement survival at swimming speeds relevant to the average daytime swimming speeds of farmed salmon (0.3–0.9 body length s^{-1}; Dempster et al., 2008; Oppedal et al., 2011), or the generally faster swimming speeds (~1.4 body length s^{-1}; Thorstad et al., 2012) with which wild salmon smolts migrate through coastal waters.

Here, we tested whether different current velocities influenced sea louse (*Lepeophtheirus salmonis*) attachment intensity and altered their post-settlement survival on post-smolt Atlantic salmon (*Salmo salar*). We made four different predictions of the effect of current velocities on sea louse initial attachment intensity, and tested different current levels to see which prediction was best supported (see Fig. 1A for detailed predictions). Further, we hypothesised that increased current velocities would reduce sea louse post-settlement survival rates. We conducted two experiments where we infested post-smolt Atlantic salmon with *L. salmonis*. Both experiments were designed to determine sea louse infestation dynamics at different current velocities; the first experiment assessed sea louse initial attachment, and the second investigated their post-settlement survival.

2. Materials and methods

2.1. Location and experimental set-up

We conducted two experiments at the Matre research station of the Institute of Marine Research, Norway. For both experiments, we used six tanks (3.0 m * 0.75 depth; volume ≈ 5 m^3) each holding a raceway (Supplementary Fig. S1). Cylindrical raceways were 0.35 m in diameter and 2.25 m long, with an internal volume of 0.2 m^3. To generate laminar flow, raceways were fitted with a propeller (Minn Kota RT80/EM, Johnson Outdoors Marine Electronics, Inc., Racine, WI, USA) with adjustable velocity followed by a honeycomb (5 mm opening, 102 mm thick, PC 5.0 G4, Plascore GmbH & Co KG, Waldlaubersheim, Germany). Plastic coated wire netting (10 * 10 mm) prohibited entry of the fish into the main tank at the openings of the raceway. An underwater video camera (SeaVision SV27, SeaVision, Fort Lauderdale, USA) was mounted in the middle of each raceway, with the field of view covering the rear of the raceway. Water temperature during experiments was 16 °C and salinity 34‰. Each raceway was continuously illuminated (24:0 light:dark regime) by a 36 W fluorescent tube suspended 35 cm above the water surface.

2.2. Experimental design

Current velocities selected for both experiments spanned the range of broad ecological relevance, from the typical swimming speeds of farmed salmon in sea-cage fish farms (Oppedal et al., 2011) to the speeds that wild salmon swim at to migrate from rivers to the open sea (Thorstad et al., 2012).

2.2.1. Experiment 1 – *L. salmonis* initial attachment intensity

To test whether different current velocities modified sea louse (*L. salmonis*) initial attachment intensity, raceways were calibrated to low (5.1 ± 0.5 cm s^{-1}; mean ± S.E.), moderate (17.0 ± 0.6 cm s^{-1}) and high (36.7 ± 1.6 cm s^{-1}) current velocities, which were equivalent to swimming speeds of 0.2, 0.7 and 1.4 body lengths (BL) s^{-1}, respectively (Supplementary Movie S1). Current velocities were measured with a Vectrino velocimeter (Nortek, Oslo, Norway) and differed among treatments (one-way ANOVA; $F_{2,9} = 242$, $P < 0.001$). This experiment was conducted in two blocks to complete four replicates for each current velocity. Experimental fish were randomly allocated into each treatment, and 10 fish were sampled 24 h after the start of the infection to calculate average infection levels used for each replicate (additional information about experimental fish, infection protocol and calculation of sea louse infection levels is provided below).

2.2.2. Experiment 2 – *L. salmonis* post-settlement survival

We tested whether different current velocities modified sea louse (*L. salmonis*) post-settlement survival after their initial

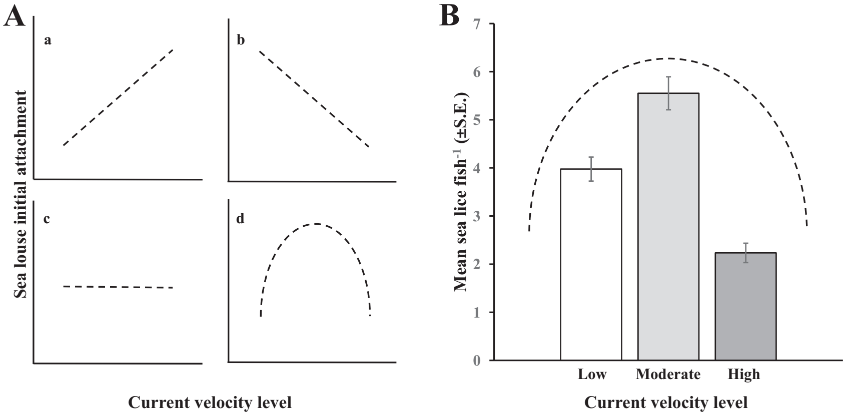

Fig. 1. Predictions and results from Experiment 1. (A) Predictions of the influence of current velocity on sea louse (*Lepeophtheirus salmonis*) initial attachment. Higher current velocities might: (a) increase initial sea louse attachment by increasing the encounter rate between the infective sea lice copepodids and salmon; (b) reduce initial sea louse attachment by decreasing the contact time necessary for successful louse attachment; (c) have no effect on initial attachment; or (d) initially increase attachment as the encounter rate increases, and then decrease attachment as contact time is reduced, hence an interaction between encounter rate and contact will determine sea louse initial attachment. (B) Experiment 1. Mean sea lice (*L. salmonis*) per fish after their initial attachment at low (5.1 ± 0.5 cm s^{-1}; mean ± S.E.), moderate (17.0 ± 0.6 cm s^{-1}; mean ± S.E.) and high (36.7 ± 1.6 cm s^{-1}; mean ± S.E.) current velocities, equivalent to swimming speeds of 0.2, 0.7 and 1.4 body lengths (BL) s^{-1}, respectively. The dashed curve on the graph represents predicted pattern d that best fits the results.