

Swimming performance of adults and copepodites of *Caligus rogercresseyi* against different water flow speeds in presence or absence of light and host fish attractants

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ABSTRACT. The present study was conducted to determine the swimming ability of adults and copepodites of *Caligus rogercresseyi* at three different water flow speeds, considering the presence or absence of attractants such as light and fish (*Salmo salar*). A total of 360 gravid females, 360 adult males, and 720 copepodites were randomly selected from a sea lice hatchery and distributed into groups. Each group was placed in a plastic bucket within a tank, and exposed or not to two attractants (light or host fish) at different water flow speeds (0, 1 and 2 cm/s). The results showed higher migration of adults and copepodites in the presence of light than in its absence ($P < 0.05$); however, no significant differences related to sea lice swimming performance were found in the presence or absence of fish ($P > 0.05$). Water flow speed had no effect on either variable ($P > 0.05$). In the current study, adult *C. rogercresseyi* demonstrated superior swimming capabilities compared with copepodites.

Keywords: Caligidosis, salmon farming, migration behavior, swimming capability, *Salmo salar*.

INTRODUCTION

Caligidosis, caused by the ectoparasite *Caligus rogercresseyi* (Copepoda: Caligidae), is considered one of the most important health problems during the seawater fattening stage of Chilean salmon farming (Feest, 2015) and represents a serious threat to its profitability, mainly due to the cost related to its surveillance and control (Sánchez et al., 2015). The disease causes economic losses estimated at US \$ 300 million a year, being approximately US \$ 80 million used for treatments (Agusti et al., 2016). The parasite feeds on mucus and epidermal and dermal fish cells (Valenzuela, 2009). Massive infections produce wounds on fish skin, causing restlessness, stress, lack of appetite, decreased growth, and immunosuppression. In addition, this parasite can act as a vector for disease-causing microorganisms such as ISAv (Oelckers et al., 2014) and Rhabdovirus Ch01 (Økland et al., 2018). Although *C. rogercresseyi* is not considered a vector for *Piscirickettsia salmonis* (Labra et al., 2020), a bacterium that substantially affects salmon farming in Chile (Piscirickettsiosis), Arriagada et al. (2019) reported that the average abundance of adult *C. rogercresseyi* has been significantly associated with the cumulative mortality caused by this bacterium in both Atlantic salmon (*Salmo salar*) and rainbow trout (*Oncorhynchus mykiss*), suggesting a synergistic relationship between the two diseases.

González & Carvajal (2003) reported that the life cycle of *C. rogercresseyi* consists in eight stages of development.

Nauplius I and II (approximately 0.45 – 0.48 mm) and copepodites (0.65 mm) are planktonic stages, with copepodites considered the infective stage. The parasitic phase begins when copepodites attach to the host and molt to chalimus I, which grows and molts to chalimus II, III, and IV until reaching the sexually mature adult stage, swimming freely over the host body surface.

In line with Genna et al. (2005), some environmental factors, such as light intensity, salinity, and host swimming speed, should influence the fixation of copepodites on the fish epidermis. In addition, Pino-Marambio et al. (2007) provided evidence that semiochemicals present in water mediate the parasite-host interaction between *C. rogercresseyi* and *S. salar*. On the other hand, Amundrud & Murray (2009) highlighted the importance of wind-driven circulation for larval sea lice transport and suggested that local environmental conditions have a considerable impact on the probability of sea lice infection spreading between wild and farmed fish populations.

The underlying hypothesis of this study was that adult *C. rogercresseyi* exhibits superior swimming capabilities compared to copepodites under identical laboratory conditions. Therefore, this study aimed to compare the swimming performances of *C. rogercresseyi* adults and copepodites under different water flow speeds, both in the presence and absence of light and fish (*S. salar*) as attractants.

†Deceased. This manuscript represents a posthumous publication of Dr. Gerold Sievers' work.

MATERIAL AND METHODS

Location

This study was conducted at the Quillaie Experimental Station (41°33'20" Lat, 72°44'00" Long), Los Lagos Region, Chile, during the austral spring of 2017.

Aquarium, fish hosts and sea lice

An aquarium (126 × 36 × 52 cm) equipped with an external Eheim-Experience 250 filter pump (12 L/min) and an Aqua Design Amano© submersible oxygenator pump (50 L/min) (Aqua Design Amano Co., Ltd.) was filled with approximately 210 L of filtered seawater. A plastic bucket (34 × 25 × 27 cm) with a capacity of 23 L with a circular opening (6.6 cm diameter) was placed on the left side of the aquarium.

Ten juvenile Atlantic salmon (*S. salar*) were randomly chosen from a fish culture tank belonging to AQUADVISE (Quillaie Experimental Station) and acclimated for 10 days before starting the trials. The mean total fish weight was 110 g, and the fish were maintained under a natural photoperiod of 12L:12D. Salinity (mean: 32 PSU), temperature (mean: 12.6 °C), and oxygen saturation (mean: 92.8%) were recorded daily. A feed ratio of 1.5% body weight, using commercial dry pellets, was considered.

A total of 360 gravid females, 360 adult males, and 720 copepodites were randomly selected from the AQUADVISE sea lice hatchery and divided into groups of 10 gravid females, 10 males, and 20 copepodites.

Experimental design

Adults and copepodites of *C. rogercresseyi* were challenged to swim from the plastic bucket to the aquarium through a circular opening during a 1-hour period under 12 different conditions: water flow speeds of 0, 1, and 2 cm/s, with variations including both the presence or absence of light and fish (*S. salar*) as attractants. Each set of 12 observations was replicated three times (R1, R2, and R3), resulting in a total of 36 observations. The overall experimental timeline spanned a total of six consecutive days.

Each observation started with the introduction of 20 adults (10 gravid females and 10 males) and 20 *C. rogercresseyi* copepodites into a plastic bucket within the aquarium, both filled with seawater. The first trial began with the presence of fish, followed by cleaning the aquarium and all its components to eliminate mucus from the water and start the trials in the absence of fish.

As illustrated in Figure 1, the water started to flow when sucked by a 70 µm filter located inside the plastic bucket, passing through the external filter-pump, and poured into the right side of the aquarium. Once there, the water flowed to the left side of the aquarium and passed through the 6.6 cm diameter opening of the plastic bucket, being sucked again by the 70 µm filter. An adjustable valve located in the external filter pump allowed different water flow speeds to be determined using a Gardena flow meter (L/min). The light was provided by an LED tube that was used to illuminate only the right side of the aquarium.

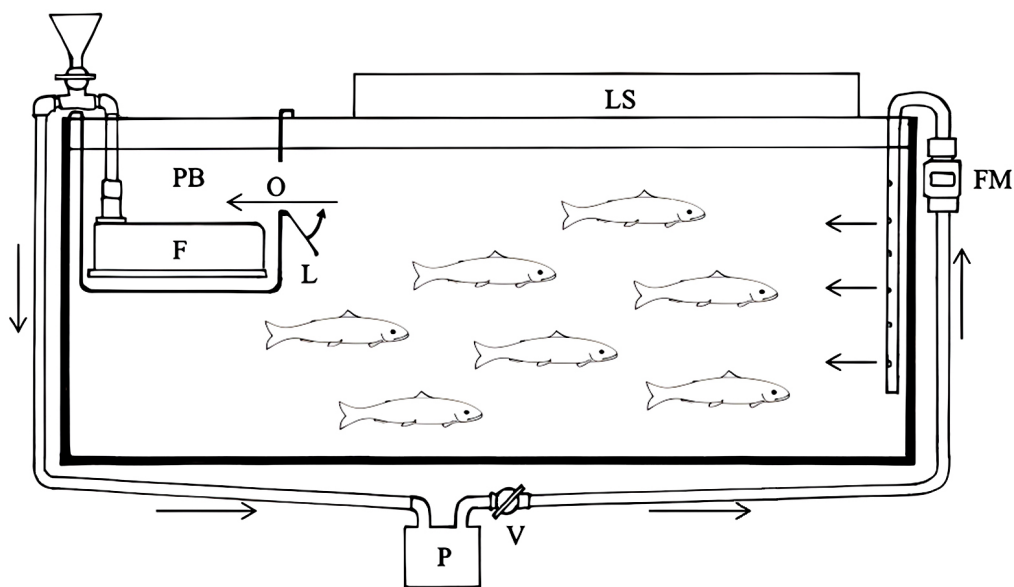


Figure 1.

Scheme of the aquarium, structure, and operational mechanisms. Water circulation is initiated by a 70 µm suction filter (F) located within the plastic bucket (PB). It then proceeds to the external filter pump (P), where a regulated flow is maintained by an adjustable valve (V) and monitored by a Gardena flow meter (FM) before being directed into the aquarium. Upon reaching the aquarium, the water cycles through the circular 6.6 cm diameter opening (O) in the plastic bucket (PB) and is subsequently drawn again by the 70 µm filter. The circular opening (O) was sealed at the end of each 1-hour observation period using the lid (L). LS represents the lighting system.

After 1 h, the circular opening of the bucket was sealed using a plastic plug, while the 70 µm filter continued to draw water from the bucket, allowing it to partially float.

Subsequently, the 70 µm filter and the walls of the plastic bucket were rinsed with fresh water to release the attached adults and copepodites into the remaining water of the bucket. This water was then passed through a 70 µm sieve to concentrate the adult parasites and copepodites. Adult parasites were carefully collected using tweezers and arranged neatly on paper to facilitate their counting. Copepodites were counted in pre-gridded petri dishes using a 10x magnification microscope. This process enabled the determination of the total number of adults and copepodites that had successfully migrated through the opening.

Statistical analysis

The analysis included a $3 \times 2 \times 2$ factorial design, along with their respective interactions, as part of a negative binomial distribution model. The first factor comprised three levels of water speed (0, 1, and 2 cm/s), whereas the second and third factors represented the presence or absence of light and fish (*S. salar*) as attractants, respectively. The age of parasites (adults/copepodites) and sex were treated as categorical variables within the same model, allowing for a comprehensive assessment of their effects on migration dynamics.

Including “age” as a fixed effect could hinder the detection of statistically significant differences in parasite migration between adults and copepodites, as it would require estimating parameters associated with each level of this variable, consuming degrees of freedom and reducing statistical power. By considering “age” as a covariate, its effect on the number of migrating parasites is adjusted, allowing the model to concentrate on the relationships between other factors, such as water flow speed and the presence or absence of light and fish. On the other hand, the sex variable was treated as a covariate instead of a fixed factor due to the inability to determine the sex of the copepodites. This approach effectively controlled the variability associated with sex, allowing for the flexible manipulation of this variable without establishing specific levels for copepodites. By adopting this method, the analysis could isolate the effects of sex more accurately, thereby enhancing the robustness of statistical evaluation.

The time elapsed from parasite harvesting to the initiation of each trial was included as a numerical covariate, considering that a longer waiting time between the parasite harvest and the start of the trials could have affected the swimming capacity of the parasites. The variable “Day” was also included to account for the specific day on which each trial was conducted. This variable was treated as a random effect in the statistical model, allowing for the assessment of any potential temporal effects and slight environmental variations, such as changes in photoperiod, salinity, temperature, or oxygen saturation, that may influence the swimming performance of the parasites.

The replicates were treated as repeated measures given that each set of observations originated from the same experimental conditions. Consequently, the random effect associated with the variable “Day” also contributed to accounting for variability among the different replicates.

The normal distribution of the data was validated using the Shapiro-Wilk test from the SAS® statistical package version 9.3, with P-values < 0.05 for both adults and copepodites. PROC GLIMMIX in SAS® was employed, relying on both Poisson and negative binomial distributions. Ultimately, the results from the models based on negative binomial distribution were used.

RESULTS

Overall, a greater number of adults migrated than copepodites, particularly in the presence of light, regardless of the water speed tested. No differences were observed in the migration between adults and copepodites in relation to the presence or absence of fish (Table 1).

By analyzing each specific combination of variables separately, a higher migration of adults compared to copepodites was observed in the presence of light compared to its absence, especially when fish were present rather than absent, at water flow speeds of 0 and 1 cm/s (Table 2).

The probability of migration was significantly higher in the presence of light than in its absence for both adults ($P < 0.0001$) and copepodites ($P = 0.0015$). However, the migration probability for both adults and copepodites was not affected by the presence or absence of fish or by the different water speed conditions ($P = 0.1238$ in adults; $P = 0.3522$ in copepodites). The interaction between fish and water speed was significant only for copepodites ($P = 0.0033$) but not for adults ($P = 0.1059$) (Table 3).

There were no statistically significant differences in parasite migration according to the variable sex, regardless of the combination of the other factors analyzed ($P > 0.05$). Additionally, neither the time elapsed from parasite harvesting to the initiation of each trial nor the variable “Day” had a statistically significant effect on the migration of the parasites ($P > 0.05$ for both).

DISCUSSION

The infection process, which is crucial for the survival of all parasite species, requires each parasitic species to ensure temporal and spatial alignment of their infective stages in the presence of the host (Sievers, G., personal communication, July 21st, 2017). *C. rogercresseyi* follows a direct life cycle in fish, involving both obligate and free-living parasitic stages. Gravid females typically carry an average of 29 ± 3 eggs in each of their two egg strings (Jaramillo et al., 2015), and the infection dynamics of fish by *C. rogercresseyi* are influenced by the ability of copepodites to locate their host (Asencio, 2015). However, this process is time-limited by the endogenous energy

Table 1.

Ability to migrate (expressed as mean and median of the three replicates) in presence or absence of light, presence or absence of fish and three different water flow speed conditions for adults and copepodites of *C. rogercresseyi*.

	Light		Fish		Water flow speed			General
	presence	absence	presence	absence	0 cm/s	1 cm/s	2 cm/s	
n	18	18	18	18	12	12	12	36
Adults								
Mean	11.1	2	7.2	5.9	8	6.3	5.4	6.6
Median	13	1	6.5	6.5	7.5	5	3.5	6.5
Copepodites								
Mean	5.8	3.1	4.6	4.3	5.4	3.8	4.2	4.4
Median	5.5	3	3.5	4.5	5	3	4	4

cm/s = centimeters per second. In the "n" row, each value represents the total number of observations (each 1-hour trial) for each combination of variables. For example, the first value in the table (n=18; light presence) is obtained by multiplying by three (three replicates) the sum of: 2 trials with light at 0 cm/s (one with fish and one without fish), 2 trials with light at 1 cm/s (one with fish and one without fish), and 2 trials with light at 2 cm/s (one with fish and one without fish). This applies to each "n=18", according to its corresponding combination of variables. For "n=12", and using "Water flow speed=0 cm/s" as an example, it is obtained by multiplying by three the sum of: no light, no fish at 0 cm/s; no light, fish at 0 cm/s; light, no fish at 0 cm/s; and light, fish at 0 cm/s. This applies to each "n=12" based on its corresponding combination of variables. The other values in these columns reflect the number of adults and copepodites, expressed as both mean and median, that migrated from the plastic bucket to the aquarium during the total number of trials for each combination of variables "n". The value "n=36" in the "General" column represents the total number of possible combinations (12) multiplied by three, i.e., the total number of observations conducted during the study. The other values in this column represent the mean and median of the previous columns for both adults and copepodites.

Table 2.

The Ability of *C. rogercresseyi* adults and copepodites to migrate (expressed as the median of the three replicates) in the presence or absence of light, presence or absence of fish, and three different water flow speed conditions. The values in this table represent the number of adults and copepodites that migrated from the plastic bucket to the aquarium, expressed as the median across the three replicates of each 1-hour trial for each possible combination of variables.

	Light	Fish	Water flow speed		
			0 cm/s	1 cm/s	2 cm/s
Adults	presence	presence	15	13	9
		absence	8	7	11
	absence	presence	3	0	0
		absence	2	0	2
Copepodites	presence	presence	10	9	3
		absence	4	3	9
	absence	presence	3	2	1
		absence	5	0	6

cm/s = centimeters per second.

reserves of copepodites, which constrain their capacity to find and infect a host (Boxaspen, 2006).

Amundrud & Murray (2009) emphasized how wind-driven circulation affects sea lice transport and infection spread between wild and farmed fish, highlighting the role of local environmental conditions. However, even with this taken into account, the limited quantity of infective forms produced by each female, the brief lifespan of the copepodites in plankton, and the widespread presence and expansion of this parasitosis may suggest that the infection process is highly successful and not contingent on external hazards.

Pino-Marambio *et al.* (2007) demonstrated that semiochemicals present in water play a mediating role in the parasite-host interaction between *C. rogercresseyi* and *S. salar*, similar to the relationship observed between *Lepeophtheirus salmonis* and its conspecific females and host fish. In the present study, the migration probability for both adults and copepodites of *C. rogercresseyi* was not influenced by the presence or absence of fish when considered as a single variable. However, the higher migration observed in adults and copepodites in the presence of light—particularly when fish were present rather than absent—at water flow speeds of 0 and 1 cm/s, supports the idea that semiochemicals play a significant role in the parasite-host interaction. The fact that this difference was only noted in the presence of light suggests that light acts as a primary stimulus for *C. rogercresseyi*, prompting the parasite to use its chemosensory systems to locate a suitable host to infect.

The finding that light emerged as a more influential factor than the presence of fish and water speed for both adult ($P < 0.05$) and copepodite migration ($P < 0.05$) supports the phototactic nature of sea lice, as previously documented by Genna *et al.* (2005). If both adults and copepodites of *C. rogercresseyi* are drawn to light, but adults display a greater proclivity for swimming and migration, this suggests that adult parasites may play a significant role in the infection process. Moreover, gravid females may potentially deposit egg strings on the surface of the host fish, with the nauplius I, nauplius II, and copepodite stages persisting within the fish's mucus until they molt into chalimus I, thereby establishing a permanent attachment to the host's scales using the frontal filament until reaching the sexually mature adult stage. This would mean that both the copepodite and the adult stage are infective. Nevertheless, for this to be possible, the time elapsed between the release of the egg strings by adult females and the emergence of the copepodites must be brief. This is particularly important given that the host's continuous mucus renewal may cause both egg strings and nauplius stages adhering to it to be expelled into the water, thus hindering copepodites from emerging within the mucus and initiating the infection process.

According to González & Carvajal (2003), under laboratory conditions, most larvae reach the nauplius II stage by day three of the planktonic phase, with the first copepodites beginning to emerge. By days 5–7, nearly all larvae had moulted into copepodites, which were ready to settle with-

in approximately 5 days at 16.5 °C, 7 days at 9.8 °C, and 9 days at 12.1 °C. This suggests that, particularly during warmer summer temperatures, larvae may have sufficient time to moult into copepodites within the mucus and settle on the host using their hooked pair of antennae. Subsequently, during moulting, they extrude their frontal filaments to establish a permanent attachment to the fish, as previously described by González and Carvajal (2003). Further studies are necessary to experimentally validate this and to gain a more comprehensive understanding of the roles of adults and copepodites of *C. rogercresseyi* in fish infections.

C. rogercresseyi is a parasite found in free-living fishes, such as *Eleginops maclovinus*, *Odontesthes regia*, and *Paralichthys microps*. Initially, the parasite adapted to cultivated *O. mykiss*, subsequently extending its adaptation to *S. salar* (Carvajal *et al.*, 1998; Bravo, 2003). This adaptation is particularly favoured by high fish stocking densities on farms, resulting in high prevalence and infection intensities (González *et al.*, 2000). Furthermore, the close proximity of salmon farms has facilitated the development and spread of caligidosis in all geographical areas where this activity occurs (Bravo *et al.*, 2008).

Caligidosis in Chile is primarily controlled by the application of chemical treatments to fish to diminish the population of adult parasites during their reproductive phase. However, this method of control has led to the emergence of parasite resistance to key drugs employed since the 1980s. The assumption that parasite sensitivity to various chemical products can be restored through the native fish fauna harbouring a sensitive parasite population seems implausible. In fact, the potential role of salmon farms as major reservoirs for resistant parasite strains raises concerns, suggesting that local fish fauna could be extensively infected by these resistant strains.

The superior migratory capacity of adults compared to copepodites reported in this study does not suggest that control strategies such as chemical treatments should focus on adult parasites. In fact, since both male and female *C. rogercresseyi* adults have the ability to detach from the host fish (González & Carvajal, 2003), they may be able to swim through the water column and locate new hosts when exposed to adverse environmental conditions. In contrast, the copepodite extrudes its frontal filament to permanently attach itself to the fish until it reaches the sexually mature adult stage and cannot detach from the host (González & Carvajal, 2003), which creates a significant opportunity for chemical treatments, especially during winter when adverse environmental conditions make the parasite more vulnerable.

In conclusion, light was identified as an attractant for both adult and copepodites of *C. rogercresseyi*, irrespective of the water speed (0, 1, or 2 cm/s) used. A higher number of adults migrated compared to copepodites, especially in the presence of light rather than absence. The presence of fish did not significantly affect sea lice migration behaviour ($P > 0.05$). Overall, adult *C. rogercresseyi* demonstrated superior swimming capabilities compared with copepodites

under identical laboratory conditions. Further research is needed to better understand the roles of *C. rogercresseyi* adults and copepodites in fish infections.

Competing interests

The authors declare that they have no competing interests.

Author contributions

G.S. contributed to the conception, design, and methodology of the study. All study materials were provided by G.S. and both authors worked together during the experimental trials. J.N. conducted the literature search, and the initial draft of the manuscript was authored by G.S. Both authors participated in the critical revision of the later version of the manuscript. G.S. designed Figure 1. As this is a posthumous article regarding the main author, J.N. was the only author who worked on the final version of the manuscript. However, no significant modifications were made to the latest version, which was jointly developed by both authors.

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