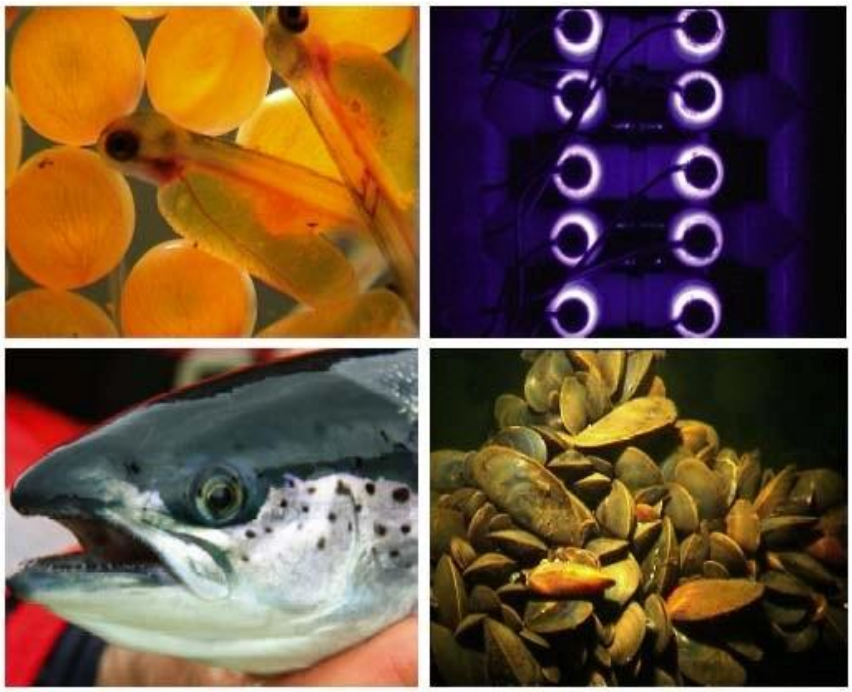
SARF108 - Literature review of key factors influencing the production, survival and infectivity of larval sea lice, *Lepeophtheirus salmonis*



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AND PREPARED BY

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SARF108

January 2015

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I. Project Details

Representatives

SARF: Mr Richard Slaski

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Contractor's address: Institute of Aquaculture, University of Stirling, Stirling, FK9 4LA

Date of commencement: 1st November 2014

Date of completion: 31st January 2015

Project costs

Requested funds from SARF were **£18,674** with additional in-kind contribution of £6226 from University of Stirling and £3500 from Institute of Marine Research, Bergen. The total project spend from SARF funding has been **£18,126** in total.

Staff input

Grade 10.49: 0.04 years

Grade 6.22: 0.3 years

Scientific Objectives

1. To produce a literature review that captures the current state of knowledge concerning the production and mortality of free-swimming nauplius and copepodid sea lice larvae and the factors affecting the infectivity of copepodids. The review will further establish what is generally known about predation in plankton in order to provide supporting data relevant to the fate of sea lice larvae in the ocean. This review will encompass peer-reviewed and grey literature as well as expert commentary.

2. To produce a final report incorporating a summary of knowledge of larval production, mortality and infectivity obtained from the literature, which may be incorporated into new mathematical models in order to better predict risk of infection and improve management strategies.

Milestones

Milestone	Target date	Title
1	15.01.2015 (2.5 months)	Completion of literature review
2	31.01.2015 (3 months)	Completion of final report

II. Executive Summary

Current sea louse models attempt to estimate louse burdens on wild and cultured salmon by predicting the production and distribution of lice larvae originating from salmon farms and estimating the subsequent risk of transmission. While physical characteristics of water bodies and weather can often be relatively accurately modelled using modern technology and sampling techniques, many aspects of sea lice biology require further parameterisation for inclusion in these models. Therefore, the objectives of this review were first, to describe current knowledge regarding the production, recruitment and survival of free-swimming sea lice larvae and the factors that affect the longevity and infectivity of copepodids and second, to identify gaps in knowledge and to suggest research approaches to filling them.

The main findings of this study were:

- Larval production is a key variable in determining the number of copepodids available for infection. Temperature is a major determinant of fecundity and hatching, with significantly more eggs being produced in winter than in summer, although eggs develop faster at higher temperatures.
- Hatching rate and success are influenced by temperature and salinity, although even under optimum conditions, a considerable proportion fail to hatch.
- Larval development times are strongly dependent on temperature, with reported times for post-hatch development to copepodid ranging from 4.6 days at 10 °C to 68.5 days at 2 °C.
- Survival is highly dependent on temperature and salinity, and larvae do not survive below 15 ‰.
- Survival is inversely related to temperature, and the maximum survival reported is 18 days at 10 °C.
- Copepodids avoid salinities <27‰ and are likely to aggregate below haloclines.
- Copepodids exhibit a diel vertical migration, which may bring them into contact with potential hosts.
- While copepodids use a combination of chemical and physical cues to locate hosts at small-to-medium scales, they are dependent on currents to disperse them over large scales.
- Copepodids have a variable infectivity profile with individuals 11–15 days post-hatch having the greatest infection capabilities.
- In experimental infection challenges under optimal conditions, infection success is frequently less than 50%; in field conditions it is likely to be considerably lower.
- Considering the level of predation of other planktonic species, larval sea lice mortality through predation is likely to be high and will vary seasonally according to local plankton assemblages.

A number of major gaps have been identified in our knowledge of the variables affecting levels of sea louse infections, and those that are likely to have the greatest impact on infection levels are (a) egg production, viability and hatching success, (b) predation in plankton and (c) copepodid infectivity profiles. A key problem identified with respect to current parameter estimates is that they derive from a broad range of sources and have been determined using a variety of differing experimental approaches. This is a barrier to the provision of "best" or consensus estimates for use in modelling. Further and more consistent data collection and experimentation will help to fill these gaps, and recommendations for further research arising from the current review are (a) a programme of farm sampling to determine egg production rates and laboratory studies to investigate the effect of controllable factors on hatching success, (b) mesocosm studies in different seasons and locations to determine levels of predation of sea lice larvae, and (c) infection experiments under different conditions of temperature, salinity and current speed to determine real-world infection success. Furthermore, co-ordinated international efforts are required in order to generate a more complete and consistent picture of sea louse infections in all regions experiencing problems with sea lice.

1 Introduction

The parasitic copepods known as sea lice remain a key constraint to the continued growth of salmonid aquaculture industries worldwide. In the North Atlantic, *Lepeophtheirus salmonis salmonis* (Krøyer, 1837) is the primary species infecting cultured Atlantic salmon (*Salmo salar* L.), although *Caligus elongatus* von Nordmann, 1832 also has some impact. Estimated costs for the Scottish industry alone were estimated to be £27M per annum in 2009 (Costello, 2009), a figure that is likely to have risen with the increasing resistance of sea lice to chemical treatments.

Current integrated pest management (IPM) strategies for sea lice control rely on a small number of licensed pesticides, of which few are effective against all stages of the parasite's life cycle, combined with effective husbandry management tools, such as single-cohort stocking, optimised stocking densities, the use of cleaner fish in polyculture and fallow periods (Skiftesvik *et al.*, 2013; Leclercq, *et al.*, 2013). The timing of management decisions is critical to the successful control of the parasite. In addition to wild hosts, as there are often several farms in a single loch (or fjord) system that can all act as point sources of sea lice, the key to predicting fluxes in lice populations is understanding the production, survival, dispersal and infectivity of the free-swimming non-infective nauplii and infective copepodid larval stages. However, despite more than three decades of research, knowledge in this area remains extremely poor.

Within the past ten years, several models have been developed that attempt to estimate lice burdens on wild and cultured salmon by predicting the production and distribution of lice larvae from salmon farms and the subsequent risk of transmission. A model provides estimates that empirical observations can be compared against and can provide insights into specific biological and hydrodynamic processes in the real world. Although complex physical coastal processes can now be accurately modelled, aspects of larval behaviour and mortality often appear oversimplified. This knowledge gap has serious consequences as it confounds the realistic estimation of the number of lice capable of infecting wild and cultured salmonid populations.

In ecological terms, sea lice can be considered r-strategists, which are characterised by small body sizes, high fecundities and short generation times. Although offspring are dispersed widely, they have a low probability of survival. However, sea lice differ from many other r-strategists in that they are attached to a host, which provides a permanent food source, allowing anomalies in sea lice such as a larger body size and raising the question of whether they have a high fecundity because they experience heavy losses during the larval stages or because they have an essentially unlimited food source? Because of the importance of high fecundity and wide larval dispersal, these are in turn key

aspects of the sea lice life cycle that determine their overall survival and success. As a result, this period of the life cycle should be the focus of efforts to predict lice burdens on fish. In the life cycle of the sea louse, however, the free-swimming stages are essentially a 'black box' that cannot be easily observed directly from field studies, and it is during this period that most variability occurs. Once a copepodid has attached to a host, it is relatively stable and likely to mature, as development after infection is unaffected by copepodid age at infection (Tucker *et al.*, 2000a; Pedersen, 2009)). Consequently, quantifying the risk of transmission is still a contentious issue with disagreement over whether lice are accumulated at their source (*e.g.* Krkošek *et al.*, 2005 and implied by Jansen *et al.*, 2012) or spread over large distances (*e.g.* Brooks, 2005; Asplin, 2014). Therefore, accurate data are urgently needed to generate more realistic models of larval dispersion and infectivity that combine physical processes with key aspects of lice biology to successfully predict larval dispersion and infection risk.

Early models for predicting lice burdens rely on the relationship between gravid female lice and infective larval stages, based on factors such as fecundity, mortality and moult timings, to predict future cohorts of lice available to infect fish (*e.g.* Heuch & Mo, 2001; Murray, 2002; Tucker *et al.*, 2002). Some models also predict the effect of various chemotherapeutic lice treatments in order to calculate the optimum treatment time (*e.g.* McKenzie *et al.*, 2002; Revie *et al.*, 2005). Although these models can predict louse numbers within a simple closed system, they cannot be applied to large open systems, such as fjordic sea lochs where salmon are commonly farmed, as they do not take into account larval dispersion.

Particle tracking models have been used by physical oceanographers for many years and are also currently used in aquaculture to predict the dispersal of particulate waste from marine cage fish farms (*e.g.* Cromey *et al.*, 2002; Corner *et al.*, 2006). These models predict the dispersal over time of particles from a point source using a hydrodynamic model, which calculates local current velocities based on fluid dynamics, external forcing from tidal elevation, freshwater inputs and wind-generated currents, and local topography. Early attempts to predict the dispersal of sea lice larvae using a particle tracking model were made by Asplin *et al.*, 2004 who estimated the dispersal of lice from a salmon farm in Sognefjord, Norway. Detailed currents, hydrography and wind forcing are calculated using high-resolution, three-dimensional ocean and atmospheric models, and although a temperature-dependant larval growth model is included, there is no estimation of larval mortality or behaviour. It assumes that lice are immortal with passive behaviour, and consequently, the dispersal of lice is overestimated with larvae being spread over a distance of 100km in just a few days (Asplin *et al.*, 2004). A similar model by Murray *et al.*, 2006, who modelled the dispersion of sea lice larvae from a

salmon farm in Loch Torridon, Scotland, also makes similar assumptions, although lice are differentiated between nauplii (non-infective) and copepodids (infective).

In order to accurately estimate infection risk, it is clear that certain aspects of louse biology, such as survival, mortality and development times, need to be incorporated into these types of models, and more recent models have attempted to do this. Murray and Amundrud (2007) and Amundrud and Murray (2009) present a coupled biophysical and particle tracking model of Loch Torridon, Scotland that incorporates development times as a function of temperature and a fixed mortality rate based on laboratory observations. Based on field observations, they assume a non-homogenous distribution of lice in the water column with the majority of lice distributed in the surface layers, and they found that wind forcing was the dominant component affecting louse dispersal.

More recent models have become increasingly complex, and Asplin *et al.* (2011 and 2014) present a model of a Norwegian fjord comprising a number of sub-models: a coastal ocean model, an atmospheric model, a fjord model, and a salmon louse growth and advection model. While the salmon louse sub-model includes relevant parameters regarding stage timings, it only includes a few simple behavioural parameters, *i.e.* a diel vertical migration, limited to depths above 10 m and avoidance of salinities below 20 ‰; however, it does not calculate louse mortality. A further model by Stucchi *et al.* (2011), which models the hydrographically complex Broughton Archipelago in British Columbia, Canada, includes a comprehensive sub-model of egg production, larval development, mortality and behaviour using data from the literature, including the effects of temperature and salinity on these parameters. While it uses a general mortality coefficient to calculate natural mortality as the larvae age and moult, it does not account for mortality due to predation in the plankton. Although there was some correlation between the predicted dispersal of sea lice and field observations (plankton net tows and wild fish surveys), predicted copepodid concentrations were generally lower than those observed. In addition, a recent model similar to the one utilised by Asplin *et al.* (2014), which uses a mortality rate of 17%, predicts that larval behaviour potentially has significant effects on advection (Johnsen *et al.*, 2014). Interestingly, using a mortality of 0% did not affect the distribution of larvae, only the magnitude of their numbers (Johnsen, pers. comm.).

While these previous models have made significant progress in predicting larval dispersal in semi-enclosed water bodies, model validation with field data is difficult, and there are always discrepancies between the model output and field observations. For example, Salama *et al.* (2011) and Adams *et al.* (2012) found very few larval sea lice in plankton tows in areas where models had predicted high numbers. However, correlation between predicted and observed infections appear to be more

accurate for the model developed by Asplin and colleagues (Sandvik, *et al*., 2014). Model variables are based on the best available data, and while accurate topography and hydrography data can easily be obtained, detailed information regarding the life history of sea lice is often lacking, despite over three decades of research in this area. Where models incorporate larval mortality, for instance, they use a constant mortality at each larval stage, which may be kept constant (*e.g*. Johnsen *et al*. 2014) or vary according to salinity, *e.g.* Amundrud and Murray (2009), Adams (2012). In reality, however, larval mortality is extremely variable according to temperature, salinity, season, moult stage and predation in the plankton, *etc*. While some data are available regarding these different parameters, others are distinctly lacking, and more research is required in these areas. Acquiring experimental data on these variables will allow the more realistic parameterisation of key elements relating to abundance and infectivity of free-swimming larval sea louse stages for incorporation into models that may more accurately predict the risk of infection under various environmental conditions.

Some models are now sufficiently developed that there is a prospect of their consideration as a component of an integrated sea louse management strategy. For example, Norwegian government resource management research support, as represented by The Institute of Marine Research, is currently proposing a move to determine the scale of farming in a given area through an operational resource management system comprising application of predictive models that estimate likely louse infection intensities (Asplin, 2014), combined with a process of continuous model validation and calibration against real-world data (Bjørn *et al*. 2014).

1.1 Study aims

The aims of this review are as follows:

1. To analyse the available literature to determine current knowledge regarding the recruitment and survival of free-swimming nauplii and copepodid larvae under laboratory conditions and factors that affect the longevity and infectivity of copepodids. Where no specific data regarding sea lice is available, the wider literature will be consulted, *e.g.* predator and prey selection in plankton, to inform questions regarding the fate of sea lice larvae in the ocean.
2. To assess the remaining knowledge gaps that might be filled by experimental or field sampling studies.

1.2 Additional considerations

- While this review focuses primarily on *Lepeophtheirus salmonis spp.*, observations from other species that are problematic in salmonid aquaculture will also be noted where appropriate.
- This review also focuses principally on knowledge concerning louse larvae deriving from farmed fish, which is due to both their greater accessibility to researchers and the fact that only in farmed fish can environmental parameters be sufficiently controlled or consistently measured. Nevertheless, it is clear that some parameters, such as the number of eggs per egg string and the lipid content of eggs, will differ in lice sourced from wild fish and these will have impacts on infection.
- In the past, there has been some conflation of data arising from Atlantic and Pacific sea louse studies. With the recognition of clear genomic and phenotypic differences between these sub-species, it is clear that defined studies need to be conducted for each.

2 Larval recruitment and survival

In order to accurately predict when and how many infective copepodids are available for infection, it is necessary to quantify the rate of larval production, which is based on female fecundity, and the subsequent development and survival rates of the larvae. These are influenced by a range of biotic and abiotic factors that fluctuate seasonally and can have an impact on adult lice during mating and egg production, on eggs during development and upon larvae once they have hatched.

2.1 Fecundity

Male lice deposit a bean-shaped packet of sperm termed a 'spermatophore' on the underside of the female genital segment and sperm is transferred from here to spermatothecae where it is stored for repeated egg batches. Once adult female lice have mated on a salmonid host, they extrude a pair of long, uniseriate egg strings from their genital segment. The fecundity of sea lice varies considerably, and early observations showed that a single egg string can contain <100–700 eggs (Wootten *et al.*, 1982). Many studies have shown that exogenous factors, such as temperature, photoperiod, salinity and food availability, interact with endogenous factors to determine fecundity in crustaceans (*e.g.* Williams, 1985; Johnson & Dykeman, 1987). Variations in the levels of sea lice infection between seasons and under different environmental conditions, suggest alterations in reproductive output in response to fluctuating environmental parameters (Ritchie *et al.*, 1993).

It is clear that temperature has a strong influence on fecundity (Tully, 1989), and the number of eggs per string is positively correlated with female body size (Tully & Whelan, 1993). Heuch *et al.* (2000) found that adult female lice of wild origin in Norway were significantly larger that adult female lice of

farm origin. Despite seasonal variations, lice of wild origin in Ireland were similarly found to be significantly larger and carried approximately twice as many eggs as lice of farm origin (Tully & Whelan, 1993) A similar pattern was noted by Pike and Wadsworth (1999), who noted that female lice of wild origin produced 965 ± 30.1 eggs per egg string pair compared to 758 ± 39.4 and 297 ± 19.1 for lice originating from untreated and treated farmed salmon, respectively, on the West Coast of Ireland. At 7.2 °C, females were observed to produce a new pair of egg strings on average 11 days after the first pair were removed, while at 12.2 °C this period was reduced to 5 days, and this continued for the reproductive life of the female, with an average of 4.95 pairs of egg strings per female (Heuch *et al.*, 2000). In this experiment, the first pair of egg strings was always significantly shorter with the mean number of eggs increasing from 152 eggs per string to 285 eggs per string for subsequent egg strings, whereas Johnson and Albright (1991) recorded a mean number of eggs per string of 344.6 ± 79.8 in lice cultured at 10 °C and 30‰ originating from wild and farmed chinook salmon (*Oncorhynchus tschawytscha*) and farmed Atlantic salmon. Similarly, Gravil (1996) recorded a mean of 141.09 ± 22.19 eggs per string for the first pair of egg strings, 216.4 ± 67.59 eggs per string for the second pair of egg strings and 208.2 ± 50.97 eggs per string for the third pair of egg strings. Fecundity was found to be lower in *C. elongatus* with the number of eggs per string being 52.62 ± 17.08 in *C. elongatus* compared to 206.2 ± 74.09 in *L. salmonis* at 14 °C (Gravil, 1996). Key values for fecundity are shown in Table 1.

Table 1. Key values of fecundity in *L. salmonis* (means ± SD)

Variable	Value	Location	Reference
Egg string production rate	New pair of egg strings every 11 days at 7.2 °C and every 5 days at 12.2 °C	Norway	Heuch *et al.*, 2000
Production capacity	4.95 pairs of egg strings per female (12.2 °C)	Norway	Heuch *et al.*, 2000
No. of eggs per string/pair of strings	152 for first string and 285 for subsequent strings at 7.2 °C	Norway	Heuch *et al.*, 2000
	344.6 ± 79.8 at 10 °C	British Columbia, Canada	Johnson & Albright, 1991a
	141.09 ± 22.19 for first string	Scotland	Gravil, 1996
	216.4 ± 67.59 for second string		
	208.2 ± 50.97 for third string		

	965 ± 30.1 for wild origin lice 758 ± 39.4 for farm origin untreated lice 297 ± 19.1 for farm origin treated lice	Ireland	Pike & Wadsworth, 1999
Egg development time	17.5 days at 5 °C 8.6 days at 10 °C 5.5 days at 15 °C	British Columbia, Canada	Johnson & Albright, 1991a
	45.1 ± 0.5 days at 2 °C 35.2 ± 0.4 days at 3 °C 27.6 ± 0.2 days at 4 °C 21.6 ± 0.1 days at 5 °C 8.7 ± 0.1 days at 10 °C	Norway	Boxaspen & Næss, 2000

Ritchie *et al.* (1993) and Gravil (1996) investigated the reproductive output of *L. salmonis* from salmon farms on the West Coast of Scotland and found that the number of eggs per string was negatively correlated with temperature, with significantly more eggs being produced in winter and early spring than in summer and autumn (Figure 1). In Ritchie *et al.* (1993), the mean number of eggs per string increased significantly from 147 to 246 between October and March (temperature range 12–5 °C) before decreasing to 175 eggs per string in August (13 °C). A similar pattern was seen by Gravil (1996), who found that the number of eggs per string ranged from 194.1 ± 66.8 in October to 286.9 ± 64 in March. There appears to be a period of lag of egg string length in response to temperature as the lowest temperature was recorded in February whereas the longest egg strings were found in March, and this may reflect the time required for egg strings to develop before being extruded. According to Johnson and Albright (1991), mean egg development times were 17.5 days at 5 °C, 8.6 days at 10 °C and 5.5 days at 15 °C. In comparison, Johannessen (1978) reported egg development times of 10–14, 25 and 33–39 days at 11.5 °C, 9.5 °C and 9 °C, respectively. Boxaspen and Næss (2000) observed development times of cold-adapted *L. salmonis* collected from Norwegian salmon farms in winter and found that egg development times were 45.1 ± 0.5 days at 2 °C, 35.2 ± 0.4 days at 3 °C, 27.6 ± 0.2 days at 4 °C, 21.6 ± 0.1 days at 5 °C and 8.7 ± 0.1 days at 10 °C. While temperature has a considerable effect

on egg production and larval development, photoperiod does not appear to have any significant effect (Ritchie *et al.*, 1993; Gravil, 1996).

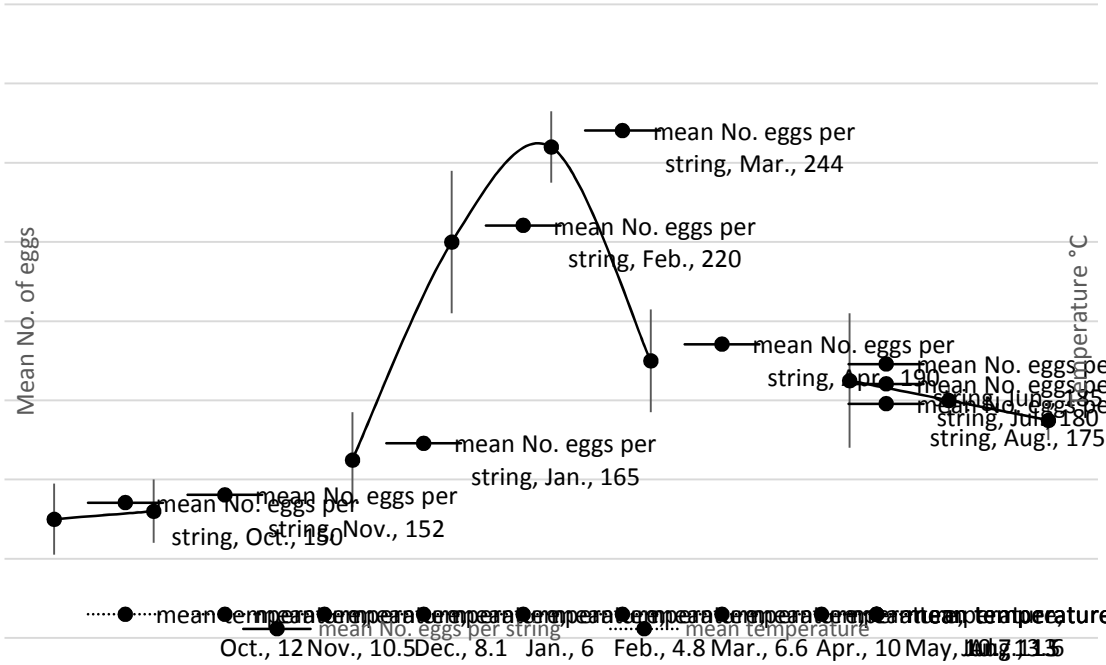

Figure 1. Relationship between water temperature and the number of eggs per egg string in *Lepeophtheirus salmonis* from salmon farms on the West Coast of Scotland. Redrawn from Ritchie *et al.*, 1993

A variety of other factors may also affect lice fecundity, although these have not been appropriately quantified. Host condition and the use of chemotherapeutants may influence egg string length and the viability of larvae (Tully & Whelan, 1993). On less favourable host species, lice may produce shorter egg strings (Johnson, 1993), and fecundity may vary on a specific host species, either as a result of diet, the physiological status of the fish or genetic variation (MacKinnon *et al.*, 1995; Mackinnon, 1998). These factors and others may account for the wide variation in the observed fecundity of lice that cannot be wholly attributed to temperature.

2.2 Hatching

Egg strings with non-viable eggs are sometimes extruded, and Heuch *et al.* (2000) found that this happened most frequently in the second and third batches of egg strings. Gravil (1996) reported that 2.1% of egg strings consisted entirely of non-viable eggs. According to Heuch *et al.* (2000), the number of viable eggs per string varied according to temperature, with a median of 13.3% of eggs being non-viable at 7.2 °C and 7.5% being non-viable at 12.2 °C. Conversely, Gravil (1996) found no correlation between egg viability and temperature in *L. salmonis* on farmed salmon on the West Coast of Scotland with a mean of 17.66 ± 23.01% non-viable eggs over one year. It is possible that the variation in egg viability found by Heuch *et al.* (2000) may be a result of maternal pre-conditioning to a particular temperature, as his experimental lice were cultured at a single temperature before being used in hatching studies, whereas those of Gravil (1996) were field-collected, which would be acclimatised to gradual changes in temperature throughout the year. In comparison, the mean number of non-viable eggs per string in *C. elongatus* was 28.19 ± 24.81%, with 18.33% of egg strings entirely consisting of non-viable eggs (Gravil, 1996).

The hatching period is variable, and Johnson and Albright (1991) report that it ranged from 18 to 65 h, with a mean of 31.7 ± 13 h for egg strings incubated at 10 °C and 30 ‰ salinity. The authors of the current review consider these to be at the extreme end of hatching periods observed.

Salinity has a considerable effect on hatching, and egg strings maintained at 10 °C and 10 ‰ salinity failed to develop in Johnson and Albright's (1991) experiments. At salinities of 15 ‰ and 20 ‰, hatching success was 70% and 78%, respectively, but only at 20 ‰ were any active nauplii produced (19.8%). At salinities of 25 ‰ and above, hatching success was 100%, but at 25 ‰ only 51.1% of nauplii were active, whereas at 30 ‰ this figure was 65.9%. Gravil (1996) reports a similar pattern with hatching success ranging from 3.27% in freshwater to 86.36% at 30‰ salinity. The effect of photoperiod was investigated by Gravil (1996), but it had no effect on hatching period or success. Key values for hatching are shown in Table 2.

Table 2. Key values of hatching in *L. salmonis*. (Means ± SD, parentheses indicate ranges)

Variable	Value	Location	Reference
Proportion non-viable egg strings	2.41% (1 yr farm samples)	Scotland	Gravil, 1996
Proportion non-viable	13.3% at 7.2 °C	Norway	Heuch et al., 2000

eggs per egg string	7.5% at 12.2 °C		
	17.66%	Scotland	Gravil, 1996
Hatching period	31.7 ± 17 hrs at 10 °C and 30‰ salinity	British Columbia, Canada	Johnson & Albright,1991a
Hatching success	0% at 10 °C and 10‰ 70% at 10 °C and 15‰ 78% at 10 °C and 20‰ 100% at 10 °C and 25‰	British Columbia, Canada	Johnson & Albright, 1991a
	3.27% at 0‰ 86.36% at 30‰	Scotland	Gravil, 1996
Active nauplii hatched	19.8% (0–89.9) active at 20‰ 51.1% (12–94.1) active at 25‰ 65.9% (9.7–95) active at 30‰	British Columbia, Canada	Johnson & Albright, 1991a

2.3 Stage timings

Development times are highly dependent on temperature. According to Johnson and Albright (1991), the average duration of the first nauplius stage was 52 h at 5 °C, 30.5 h at 10 °C and 9.2 h at 15 °C, whereas the duration of the second nauplius stage was 170.3 h at 5 °C, 56.9 h at 10 °C and 35.6 h at 15 °C for *L. salmonis oncorhynchi* Similarly, other studies report the duration of the first nauplius stage to be 35 h at 9.2 °C, 12 h at 15.5 °C (Johannssen, 1978) and 18 h at 12 °C (Wootten *et al.*, 1982) and the duration of the second nauplius stage to be 77 h at 9.2 °C, 63 h at 11 °C (Johannssen, 1978), 63 h at 11 °C, 46 h at 12 °C and 33 h at 19 °C (Wootten *et al.*, 1982). Similar times were observed by Tully (1992), who reports that the duration of both nauplius stages was 223.3 h at 5 °C, 87.4 h at 10 °C and 50.0 h at 15 °C. The time required for physically moulting (exuviation) from nauplius I to nauplius II and nauplius II to copepodid are reported as 10.53 ± 4.34 mins and 12.21 ± 3.87 mins, respectively, and during the moult the larvae are inactive and sink through the water column (Gravil, 1996).

It appears that the temperature of acclimation of adult female lice is important in determining the temperature tolerance of their eggs and larvae. Johannessen (1975) reports that in adult lice cultured at 9 °C, nauplius development occurred only between 8–11 °C, whereas acclimation at 11.5 °C allowed larval development up to 22 °C. In sea lice collected from fish farms in Norway during winter, which were acclimated to low temperatures, the total development time from hatching to copepodids was

12.7 days at 10 °C and 68.5 days at 2 °C (Boxaspen and Næss, 2000). Key values for stage timings are shown in Table 3.

Table 3. Key stage timings for *L. salmonis* (mean values)

Variable	Value	Location	Reference
Duration of first	52 h at 5 °C	British Columbia,	Johnson & Albright, 1991a
nauplius stage	30.5 h at 10 °C	Canada	
	9.2 h at 15 °C		
	35 h at 9.2 °C	Norway	Johannessen, 1978
	12 h at 15.5 °C		
	18 h at 12 °C	Scotland	Wootten *et al.*, 1982
	43.25 h at 7.5 °C	Scotland	Gravil, 1996
Duration of second	170.3 h at 5 °C	British Columbia,	Johnson & Albright, 1991a
nauplius stage	56.9 h at 10 °C	Canada	
	35.6 h at 15 °C		
	77 h at 9.2°C	Norway	Johannessen, 1978
	63 h at 11 °C		
	63 h at 11 °C	Scotland	Wootten *et al.*, 1982
	46 h at 12 °C		
	33 h at 19 °C		
Development to	12.7 days at 10 °C	Norway	Boxaspen & Næss, 2000
copepodid	68.5 days at 2 °C		
	111–177.5 h at 10 °C	Scotland	Gravil, 1996

2.4 Survival

Nauplii that hatch successfully are free swimming in the water column. At this stage they do not feed, but are lecithotrophic (yolk feeding) and rely on their energy reserves to sustain them until they moult

to infective copepodids and find a suitable host. The survival of sea lice and the rate at which they deplete their energy reserves are strongly influenced by temperature and salinity. The size of larvae and their lipid stores is also dependant on season, and Gravil (1996) reports that nauplius I larvae were largest in August with a mean body width of 214.05 µm and a mean lipid reserve width of 135.84 µm compared to 197.76 µm and 112.98 µm in May for mean body width and mean lipid reserve width, respectively. It is likely that increased energy reserves will increase the longevity of the non-feeding larval stages, although no data are available comparing survival at different times of year.

Johnson & Albright (1991a) report that active copepodids were only obtained at salinities above 30‰ at 10 °C (35.2% active), although survival was extremely variable ranging from 0–80.6% per egg string. Similarly, Gravil (1996) found that copepodids were only obtained at salinities greater than 25‰, and at 10 °C and 35‰, 18.33% reached the infective copepodid stage with nearly 50% mortality being seen in the nauplius I stage. Gravil (1996) found that sea lice larvae from Scotland did not proceed past the nauplius II stage at 5 °C, but died before moulting to copepodids, and at 7.5 °C, very few copepodids were obtained. In sea lice adapted to low temperatures, however, copepodids were obtained from 25% of egg strings reared at 2°C, 42% at 3°C, 100% at 4°C and 75% at 5°C (Boxaspen and Næss, 2000). In *C. elongatus*, Pike *et al.* (1993) report 90% survival from the nauplius stage to the copepodid stage at 15 °C with this figure decreasing to 60% at 5 °C.

As with all copepods, sea lice have preferred environmental conditions, which are determined by their physiological tolerances. Copepodids that were transferred from full-strength seawater to 5‰ salinity survived for just 3 h at 10 °C, and those transferred to 10‰ salinity survived for less than one day (Johnson & Albright, 1991a). A similar experiment by Gravil (1996) found that the median survival time was 14.87 h at 0–10‰. While copepodids can osmoregulate above 16‰, their haemolymph becomes rapidly diluted below 12‰, and they are unable to regulate cell volume and die within a few hours (Hahnenkamp & Fyhn, 1985; Pike & Wadsworth, 1999).

Once nauplii moult to copepodids, they need to find a suitable host before their lipid reserves are depleted, and the rate at which this occurs is influenced by temperature and salinity. Hyperosmotic regulation is energetically costly, and an increased energy demand significantly reduces the survival time of copepodids due to their limited energy reserves (Torres *et al.*, 2002). Johnson and Albright (1991) report that survival was prolonged at salinities of 15–30‰ and temperatures of 5–15 °C, and that mean survival times were between two and eight days. Similarly, Wootten *et al.* (1982) report that the mean survival time of copepodids at 12 °C was 4 days. In Gravil (1996), the median survival time of copepodids was 54 h at 15‰, 67 h at 20‰, 68 h at 25‰, 55 h at 30‰ and 64 h at 35‰, which

reflects the increased energy required for hyperosmotic regulation at lower salinities. Conversely, Bricknell *et al.* (2006) report the median survival time of *L. salmonis* copepodids to be 4 h at 16‰, 6 h at 19‰, 8 h at 23‰, 11 h at 26‰, 24 h at 29‰, 22 h at 33‰ and 25 h at 36‰. The reason for the differences in survival times reported in Gravil (1996) and Bricknell *et al.* (2006) is unknown, although Bricknell *et al.* used copepodids that were a few days old and cultured them with aeration whereas Gravil used unaerated containers.

According to Johnson and Albright (1991), the maximum survival time was 17 days at 10 °C and 25‰ salinity, and copepodids in lower salinities (15–20‰) were generally less active than those maintained at higher salinities (25–30‰). In full strength seawater (35‰), the maximum survival time of copepodids at 10°C was 18 days (Gravil, 1996). Due to the reduced hatching success and subsequent low survival of *L. salmonis* in low salinities, it is likely that they may be excluded from salinities less than 15‰ (Johnson & Albright, 1991a), and survival is severely compromised at salinities below 29‰ (Tucker *et al.*, 2000c). Although survival is reduced at lower salinities, short-term exposure to reduced salinities does not have a long-term impact on the development of surviving copepodids (Bricknell *et al.*, 2006). Attachment to a host was not observed to improve survival at reduced salinities (Hahnenkamp & Fyhn, 1985) and these authors suggested that, unlike adult lice, copepodid and chalimus stages are unable to use ions obtained from their host to replace those lost to a hypo-osmotic environment. However, it appears likely that, due to their small size, attached larvae will receive at least some protection from reduced salinities through boundary layer effects coupled with close contact with the host / host mucus and it is also clear that, as feeding stages, some protection would be received from ingested host tissue.

The survival time of copepodids is inversely related to temperature, and Gravil (1996) reports that the median survival times were 116 h at 5 °C, 90 h at 10 °C and 82 h at 15 °C at full salinity (35‰), which is presumably due to lower metabolism and, therefore, increased longevity of energy reserves at lower temperatures. There is, however, a seasonal investment by adult females in reproduction as nauplii are larger and have larger energy stores in summer than in winter (Gravil, 1996). At higher temperatures, metabolism is higher and larvae are more active, so their energy stores are more rapidly depleted. It is possible that the increase in the size of larvae and their energy stores in summer may be a compensatory mechanism to account for their energy stores being depleted more rapidly than in winter, which ensures that their life expectancy is similar to that at colder winter temperatures. Further experimental work is required to confirm this. Key values for survival are shown in Table 4.

Table 4. Key values of survival for *L. salmonis* larvae (50% survival times (LT_{50}) are shown unless specified otherwise)

Variable	Value	Location	Reference
Nauplius I width	214.05 µm in August 187.76 µm in May	Scotland	Gravil, 1996
Nauplius lipid reserve width	135.84 µm in August 112.98 µm in May	Scotland	Gravil, 1996
Survival to copepodid	No survival at 10 °C and less than 30‰ 35.2% at 10 °C and 30‰	British Columbia, Canada	Johnson & Albright, 1991a
	No survival at less than 25‰ 18.33% at 10 °C and 35‰	Scotland	Gravil, 1996
Copepodid Survival time	3 h at 10 °C and 5‰ Less than 1 day at 10 °C and 10‰ 2–8 days at 5–15 °C and 15–30‰ Max. of 17 days at 10 °C and 25‰	British Columbia, Canada	Johnson & Albright, 1991a
	14.87 h at 0–10‰ and 10 °C 54 h at 15‰ and 10 °C 67 h at 20‰ and 10 °C 68 h at 25‰ and 10 °C 55 h at 30‰ and 10 °C 64 h at 35‰ and 10 °C 116 h at 35‰ and 5 °C 90 h at 35‰ and 10 °C 82 h at 35‰ and 15 °C Max. of 18 days at 10 °C and 35‰	Scotland	Gravil, 1996
	4 h at 16‰ 6 h at 19‰ 8 h at 23‰ 11 h at 26‰ 24 h at 29‰ 22 h at 33‰ 25 h at 36‰	Scotland	Bricknell *et al*., 2006

4 days at 12 °C		Scotland	Wootten *et al*., 1982

3 Behaviour

The nauplius stages of sea lice are principally dispersal stages, whereas the purpose of the copepodid stage is to find and infect a suitable host. Although they are subject to water movements in the form of tides, river flows into estuaries and wind-forced currents, which serve to disperse them from their source over a wide area, they do have limited movement capabilities, and their dispersal can be partially influenced by certain behaviours, *e.g.* aggregating at particular depths in the water column. In order to maximise their chances of survival and host interception, they must be able to respond to cues present in their environment and react to them appropriately. Their behaviour can be categorised according to the following activities (Bron *et al.*, 1993):

1. Predator avoidance
2. Avoidance of adverse environmental conditions
3. Movement into or maintenance within host-rich environments
4. Host location
5. Host contact/settlement
6. Confirmation of host suitability

Cues that may play a role in influencing the behaviour of sea lice larvae are light, chemical, pressure and water flow/vibration.

Both nauplius and copepodid stages have been observed to actively swim upwards as they are negatively buoyant, and their movements are punctuated by periods of passive sinking (Bron, 1993, Gravil, 1996). Haury and Weihs (1976) suggest that this behaviour theoretically saves energy compared to continuous swimming at a fixed depth, which is particularly important to the lecithotrophic larvae of *L. salmonis*, which must conserve their limited energy reserves where possible. Despite their energy considerations, copepodids must maintain their position in the water column where their chances of encountering a host are highest (Bron, 1993). However, Gravil (1996) found that the activity of nauplii and copepodids is dependent on temperature; at 5 °C their movements were reduced and they aggregated at the bottom of containers, whereas at 10 °C and 15 °C they spent more time actively swimming than passively sinking and aggregated at the surface. Copepodids swim more rapidly than nauplii and have longer swimming periods and shorter rest periods (Bron, 1993). Gravil (1996) reports that the mean swimming speed of nauplii was 1.25 ± 0.16 cm s^{-1}, whereas the

mean swimming speed of copepodids was 2.14 ± 0.24 cm s^{-1}. The mean sinking speeds were 0.09 ± 0.01 cm s^{-1} and 0.10 ± 0.03 cm s^{-1} for nauplii and copepodids respectively. In this study, the maximum speed recorded was 10.23 cm s^{-1} when stimulated by vibration of the test chamber and gives an indication of the swimming ability of copepodids. A similar one-second burst speed of 9 cm s^{-1} was recorded by Heuch and Karlsen (1997), although speeds of 2 cm s^{-1} were sustained when stimulated.

Current speed and host swimming speed affect the ability of infecting copepodids to make initial contact with the host and to remain attached following contact. Given the respective speed of copepodids and salmonids, the former cannot pursue the host but must intercept it by burst-swimming when detecting it in the water column. The exposure time of the copepodid to the host reduces with increasing current / host swimming speed, which reduces the window of opportunity for infection. In addition, the low-flow zone (boundary layer) caused by drag at the surface of the fish, becomes thinner with increasing current / host speed, which increases the exposure of the copepodid to the ambient water flow during attachment. This means that at higher flows, the copepodid has less opportunity to make contact and is more likely to be removed from the host by the current (Bron, 1993). The greater boundary layer thickness and, hence, shelter from the ambient current offered by fin rays held perpendicular to the direction of water flow is considered to provide some explanation of the observed greater frequency of copepodid settlement on the fins of hosts (Bron, 1993, Bron *et al*. 1993). Similarly, the slower swimming speed of fish in tank challenges may explain the largely artefactual attachment of copepodids to the gills in such trials, an observation rarely made under field conditions (ibid.). While larger fish swim faster, this is offset by the provision of a larger surface area for settlement and a greater boundary layer / shelter provided by larger fins. Frenzl *et al*. (submitted 2014) observed declining numbers of attaching copepodids with increasing current speeds. For a dose of 2500 copepodids $fish^{-1}$ provided in a flume challenge, highest infection occurred at 0 cm s^{-1} (mean 8.4 copepodids per fish) and lowest at 32.6 cm s^{-1} (mean 0.2 copepodids per fish).

Little is known concerning the effects of competition for space and/or resources during initial copepodid settlement, however, Frenzl *et al*. (submitted 2014) have demonstrated a non-linear increase of infection numbers with challenge dose in flume challenges, possibly suggesting the increasing saturation of available settlement niches with increasing numbers available for infection.

Copepodids of *L. salmonis* are highly photopositive and move towards the illuminated zone of the vessel in laboratory experiments even at low light intensities (Johannessen, 1975; Wootten *et al.*, 1982; Bron *et al.*, 1993, Gravil, 1996). The nauplius stages are also photopositive, but the nauplius I stage only exhibits a positive response at light intensities of 200 lux or more, whereas this value is 85

lux in the nauplius II (Gravil, 1996). Whereas nauplii exhibit increasing activity with increasing light intensity, copepodids do not (ibid.). The free-swimming larval stages of *C. elongatus* are also phototactic, with the copepodids showing a greater response to light than the nauplii stages (Hogans & Trudeau, 1989). In *L. salmonis*, a peak response was seen at a wavelength 500nm in the nauplius II stage (Gravil, 1996) and 550 nm in the copepodid stage (Bron *et al.*, 1993, Gravil, 1996), and this corresponds to the maximum transmitted light intensity at twilight, which may be a cue for vertical migration in copepodids as suggested for free-living copepods (Forward & Douglass, 1989). In flume challenges, Frenzl *et al*. (2014 submitted) found maximum sensitivity of copepodids to lie at 455 nm. Despite clear evidence for response to shadows (scototaxis) in adult sea lice (authors' observations) there is no evidence for a shadow response in copepodid or nauplius stages.

Heuch *et al.* (1995) found a strong diel vertical migration in *L. salmonis* copepodids where they gathered near the surface during the day and spread out into deeper layers at night. Despite the recognised photopositive behaviour of copepodid stages, a number of authors observed successful settlement or attempted settlement in darkness (Johnson & Albright, 1991a; Bron *et al*., 1993, Heuch *et al*. 2007, Frenzl *et al*. 2014 submitted) although settlement success was generally lower than under illuminated states. As salmon remain in deeper waters during the day and rise to the surface at night, they swim through a population of sinking or rising copepodids every 12 h (ibid.). In addition, vertically migrating hosts produce stronger currents than resting fish, and pressure waves in front of swimming fish trigger a looping behaviour allowing nearby copepodids to avoid predation and attach to a host (rheotaxis) (Bron *et al.*, 1993; Heuch & Karlsen, 1997; Heuch *et al.* 2007). Bron *et al.* (1993) and Gravil (1996) also demonstrated that copepodids are negatively geotactic, *i.e.* they swim towards the surface as pressure increases, which also suggests that they tend to aggregate in surface waters. Presumably, these experiments were conducted with illumination, and therefore, it is not known whether copepodids would be negatively geotactic in the dark when they would normally spread out into deeper water. In the study by Heuch *et al.* (1995), 6 m deep mesocosm bags were suspended in the water column, and therefore, the vertical migrations of copepodids were limited by the depth of the bags. Zooplankton appear to scale their vertical migrations according to the available water depth (Young & Watt, 1993), so the relationship of experiments with constrained depths to the natural situation is uncertain. This has implications for the dispersal of lice by water currents as current velocity and direction often vary with depth. It is clear, however, that wind forcing can be a dominant component of sea lice dispersal (Murray & Amundrud, 2007; Amundrud & Murray, 2009), and therefore improved knowledge of the diel vertical migration of copepodids between surface and

deeper waters would allow the wind forcing component of sea louse dispersal to be predicted more accurately.

The survival and activity of sea lice is reduced at low salinities (Pike & Wadsworth, 2000; Bricknell *et al.*, 2006), and increased rainfall has been shown to lead to reduced copepodid abundance around river mouths (Costello *et al.*, 1998a). In salinities less than 21 ‰, the swimming ability of nauplii and copepodids is lost, although full activity is recovered if the exposure time is short (<5 minutes) (Gravil, 1996). Bricknell *et al.* (2006) found that copepodids actively avoided salinities lower than 27‰ by orientating themselves in a vertical sinking position and occasionally actively swimming downwards. Given a choice, they will remain in full strength seawater. It is likely that copepodids avoid areas of low salinity as they require increased energy expenditure, which reduces survival time (Torres *et al.*, 2002). Energy is expended for osmoregulation and to maintain their position in the water column as sinking rates increase with decreasing salinity (Bricknell *et al.*, 2006). As low salinities reduce the activity levels of copepodids, their ability to respond to host cues is reduced (ibid.).

It has been proposed, although supporting evidence is lacking, that copepodids may actively migrate to river mouths where high concentrations of salmon smolts are present at certain times of year, which would increase their probability of encountering a host (Carr & Whoriskey, 2004; Costello *et al.*, 2004; McKibben & Hay, 2004). Studies in estuarine areas in Ireland suggest that copepodids are not found near the mouths of rivers for the majority of the year (Costello *et al.*, 1998a), but high concentrations coincide with the seaward migration of salmon smolts and the freshwater migration of adult salmon (Costello *et al.*, 1998a; McKibben & Hay, 2004). As copepodids are capable of actively altering their position in the water column, it is possible that they may be able to use tidal transport to migrate towards river mouths, although no evidence has been found to support this. Transport towards river mouths would only be possible if copepodids rested on the sediment during the ebb tide and rose into the water column during the flood tide (Costello *et al.*, 1998a,b; Kimmerer *et al.*, 1998). As copepodids have been shown to remain active in the water column (Bron *et al.*, 1993; Heuch *et al.*, 1995; Gravil, 1996), they are distributed within a water body according to the prevailing currents and are thus unlikely to directly influence their large-scale movement towards a particular location. It is possible that the high concentration of copepodids near river mouths at some times of year is a result of hatching egg strings from lice on adult salmon that often congregate at river mouths prior to their migration upstream, particularly during periods of low river flow (Jonsson *et al.*, 1990; Smith *et al.*, 1994). Similarly, the absence of copepodids at river mouths during periods of high rainfall may simply be due to salmon migrating rapidly upstream when river flow is high (Costello *et al.*, 1998a,b).

The responses of sea lice copepodids to physical cues, such as light and salinity, enable them to gather in areas where host fish are likely to be found, and mechanical cues enable them to infect a host. Chemoreception also plays an important role in host location, with copepodids employing the cues provided by kairomones, specific chemicals released by host fish, to improve the probability of host encounter. Copepodids swim with a general search pattern, but once a host odour has been detected, a host-encounter search pattern is switched on, which consists of increased duration and frequency of turning during the normal sinking and swimming behaviour (Genna, 2002). A directional component, or rheotaxis, is also apparent whereby activated copepodids swim towards a suitable odour source over a distance of centimetres (Bailey *et al.*, 2006), although a group of salmon might initiate a response over a scale of metres (Mordue Luntz & Birkett, 2009). Experiments have shown that *L. salmonis* copepodids are attracted to odours from salmon and sea trout, and behavioural activation and positive upstream rheotaxis occur in the presence of salmon-derived compounds (Devine *et al.*, 2000; Genna, 2002; Ingvarsdottir *et al.*, 2002; Bailey *et al.*, 2006). Non-host odours activate copepodids, but positive rheotactic movements are not observed, indicating that *L. salmonis* can discriminate between salmonid hosts and other non-host fish from their odour trails (Bailey *et al.*, 2006). In comparison, *C. elongatus*, which is a generalist and infects many different species of fish, demonstrates behavioural changes to chemical cues from a wide range of fish, although physical cues may be more dominant in this species (Mordue Luntz & Birkett, 2009). Although the activity of copepodids is affected by temperature, with reduced activity at lower temperatures, it is not known whether low temperatures affect the switch to host-seeking behaviour and the distance over which they may be able to detect host cues.

Despite their avoidance of areas of low salinity, the use of haloclines by copepodids has been proposed as a host-finding mechanism, since host odours may accumulate in thin layers where a density gradient occurs (Heuch, 1995). In this respect, 80% of copepodids were observed to aggregate at the confluence of a 15-30‰ step-salinity gradient in laboratory experiments (Heuch, 1995). In addition, positioning close to a halocline may increase the chance of encountering a host, as salmon have been observed to follow salinity gradients (Lyse *et al.*, 1998; Finstad *et al.*, 2000). Key values for behaviour are shown in Table 5.

Table 5. Key variables of behaviour in *L. salmonis* larvae.

Variable	Value	Reference

Nauplius mean swimming speed	1.25 ± 0.16 cm s^{-1}	Gravil, 1996
Nauplius mean sinking speed	0.09 ± 0.01 cm s^{-1}	Gravil, 1996
Copepodid mean swimming speed	2.14 ± 0.24 cm s^{-1}	Gravil, 1996
Copepodid max. swimming speed	10.23 cm s^{-1}	Gravil, 1996
	9 cm s^{-1}	Heuch & Karlsen, 1997
Copepodid mean sinking speed	0.10 ± 0.03 cm s^{-1}	Gravil, 1996
Light	Positive phototaxis in nauplii peaked at 500 nm. No response below 200 lux in nauplius I and below 85 lux in nauplius II. Increasing response with increasing intensity.	Gravil, 1996
	Positive response in copepodids peaked at 550 nm. Equal response to all light intensities	Bron *et al.*, 1993; Gravil, 1996
	Diel vertical migration - aggregate at surface during day and spread into deeper water at night.	Heuch *et al.*, 1995
Currents	Pressure waves in front of swimming fish triggers looping behaviour of copepodids allowing them to attach to a host.	Bron *et al.*, 1993; Heuch & Karlsen, 1997; Heuch *et al.*, 2007
Pressure	Negative geotaxis as copepodids swim towards surface as pressure increases.	Bron *et al.*, 1993; Gravil, 1996
Temperature	Reduced activity at 5 °C and aggregate at bottom of containers	Gravil, 1996
	Active swimming at 10 °C and 15 °C and aggregate near surface	
Salinity	Nauplii and copepodids lose swimming ability at salinities < 21‰	Gravil, 1996
	Copepodids prefer full-strength seawater and avoid salinities <27‰	Bricknell *et al.*, 2006

	Reduced activity and host-seeking ability at low salinities	Bricknell *et al.*, 2006
	Aggregation of copepodids below haloclines	Heuch, 1995
Host odours	Switch on host-encounter search pattern in copepodids Positive rheotaxis over several cm for single host or several m for group of hosts	Devine *et al.*, 2000; Genna, 2002; Ingvarsdottir *et al.*, 2002; Bailey *et al.*, 2006; Mordue Luntz & Birkett, 2009

4 Infectivity

While most previous models of sea lice dispersion include a mortality factor, they do not account for variations in infectivity. It is incorrect to assume that, once the copepodid stage is reached, 100% infection will occur (Gravil, 1996). Dispersion on currents and host location behaviour bring the copepodids into the same locality as potential hosts, but the process of infection is influenced by various factors, including salinity, temperature, season, a range of host factors and copepodid age.

As lecithotrophic larval stages are reliant on their energy reserves for swimming, moulting and host infection, the excessive depletion of these reserves prior to infection can result in the loss of infective capability. As copepodids age, a higher proportion display reduced activity due to the depletion of energy reserves or senescence (Bron, 1993). Gravil (1996) found that the mean size of lipid vesicles in the mid-gut of copepodids was significantly reduced after seven days, and Tucker *et al.* (2000a) reports a significant reduction in the calorific value of *L. salmonis* larvae over seven days with a sharp decline after five days. By measuring stored lipid volume, it is possible to determine age and viability in individual copepodids, and these can be divided into three loose categories: early copepodids with an apparent increase in lipid volume reflecting incorporation of naupliar lipids into distinct vesicles in the gut; mid-life copepodids, which show a downward trend in lipid levels and may be the most active individuals with mature infective capabilities; and late copepodids with low reserves of lipid, which may be less capable of infection (Cook *et al.*, 2010). The depletion of energy reserves, which consist primarily of lipids, might also result in a loss of buoyancy, making swimming more energetically costly (Bron, 1993), although Gravil (1996) found no evidence to support this. Gravil (1996) observed three stages of activity: newly moulted copepodids swam in spontaneous bursts without stimulation; at eight days at 10 °C, 50% of copepodids were only active when stimulated; after eight days remaining copepodids only showed activity after being stimulated by a water jet from a pipette. This suggests that copepodids may adopt a strategy of energy conservation if a host is not located after a certain

period of time, and that by only becoming active when stimulated, they preserve their remaining energy stores as long as possible.

This reduced activity level affects infectivity, and Gravil (1996) reports that copepodid infection success at 10 °C and 35‰ salinity was 22.22 ± 8.32% at one day old and 14 ± 8.71% at seven days old. At seven days old, approximately 20% of copepodids were active without stimulation and 40% were active with or without stimulation. Bron (1993) reports similar infection rates with 23.2% settlement under illuminated conditions and 18.4% settlement in the dark for 1–3-day-old copepodids, although there was no significant difference in settlement between light and dark conditions. For a cohort of copepodids hatched within 24 h, Frenzl *et al*. (submitted 2014) found in flume challenges that maximal infectivity was obtained at 4 days post-moult to copepodid, with infectivity of the cohort declining by 6 days through mortalities and lower infective capabilities. Tucker *et al.* (2000a) found that infection success was approximately 75% at summer temperatures (11 °C) and approximately 20% at Scottish winter temperatures (6.5 °C) in one and three-day-old copepodids, with infection success declining significantly in five-day-old copepodids, although lice in this experiment were collected and cultured at 10 °C before being used in experiments, which may have affected the results. The ability of copepodids to infect hosts past seven days old is not known, and further experimentation is required to determine this. However, infection success is clearly linked to both the longevity and activity of the copepodid stage. Despite infection success being dependent on copepodid age, the survival of copepodids once attached to a host does not differ between copepodids that infect at different ages (Tucker *et al.*, 2000a; Pedersen, 2009), which is likely due to the commencement of feeding once attached to a host. This underlines the fact that the key determinants of variability of larval infection levels in Atlantic salmon largely act prior to host settlement *i.e*. within the black box comprising egg production to host contact. Because some Pacific salmon species, *e.g*. juvenile coho, are, in contrast able to mount a successful inflammatory response to infecting copepodids (Johnson and Albright, 1992; Fast *et al*. 2002; Jones, 2011), the host may play a greater role in mediating infection success in these host species.

Host settlement success is also reduced at lower salinities, which coincides with a decrease in their energy reserves (Tucker *et al.*, 2000a,b; Bricknell *et al.*, 2006). It is likely that the physiological stress associated with reduced salinity rapidly depletes the energy reserves of copepodids, which causes premature senescence and results in levels of settlement success similar to those found in older copepodids (Bricknell *et al.*, 2006). These authors report that infection levels were reduced by 55% at 26‰ (~14% infection), 55% at 19‰ (~10% infection) and 87.5% at 12‰ (~1% infection) compared to

full-strength seawater, which cannot be fully attributed to reduced survival at these salinities; at 4‰ no copepodids were found on the fish. Key values for infectivity are shown in Table 6.

Table 6. Key variables of infectivity in *L. salmonis* larvae.

Variable	Value	Reference
Infectivity with age	Early copepodids: 7–10 days post-hatch at 12 °C increasing infective capabilities	Cook *et al.*, 2010; Bron, 1993; Gravil, 1996; Tucker *et al.*, 2000a
	Mid-life copepodids: 11–15 days post-hatch at 12 °C; decreasing lipid and mature infective capabilities	
	Late copepodids: 16–20 days post-hatch at 12 °C; low lipid reserves and less capable of infection	
Infection success	22.22 ± 8.32% at 1 day old, 10 °C and 35‰	Gravil, 1996
	14 ± 8.71% at 7 days old, 10 °C and 35‰	
	23.2% in 1–3-day-old copepodids in light	Bron, 1993
	18.4% in 1–3-day-old copepodids in dark	
	Maximum infection at 4-day-old copepodids	Frenzl *et al.*, 2014
	~75% at 11 °C and ~20% at 6.5 °C in 1- and 3-day-old copepodids	Tucker *et al.*, 2000a
	At 12 °C: ~31% at 34‰	Bricknell *et al.*, 2006
	~14% at 26‰	
	~10% at 19‰	
	~1% at 12‰	
	No infection at 4‰	

5 Mortality through predation

Once sea lice have attached to a host, their chances of survival are high as they have a constant food supply and external factors affecting survival are relatively few, *e.g.* adverse environmental conditions, host immune response and predation by cleaner fish. During their free-swimming planktonic stages, however, they form a part of a complex plankton food web and are subject to selective and non-selective predation by other planktonts and sessile filter feeders such as bivalve molluscs. Global approximations of the partitioning of zooplankton mortality suggest that predation mortality accounts for 67–75% of total mortality in the plankton (Hirst & Kiørboe, 2002). Although predation is likely to have a significant impact on sea lice survival, there are currently no estimates of sea lice predation mortality in the literature due to the difficulty in obtaining this kind of information. Some sea lice dispersion models do include a fixed mortality rate for the free-swimming stages, *e.g.* Amundrud and Murray (2009) used a fixed mortality rate of 0.01 h^{-1} for nauplii and copepodids. Providing an estimate of predation mortality is difficult as there are a wide range of prey selection sizes amongst the different actively or passively predating species represented in the zooplankton community, these being influenced by feeding mode and predator size (Hansen *et al.*, 1994; Wirtz, 2011, Wirtz, 2012), and plankton assemblages also vary considerably according to season and location (*e.g.* Daewel *et al.*, 2014).

5.1 Plankton community structure

In regional marine ecosystems, several processes govern the structure and dynamics of plankton communities, which can be subject to either bottom-up control (resource limitation) or predation by higher trophic levels (top-down control) (Daewel *et al.*, 2014). These processes vary according to geographical location resulting in distinct ocean regions with their own typical plankton assemblages. In mid-latitude continental shelf regions where sea lice are found, spring algal blooms drive productivity after winter mixing, followed by summer stratification and low productivity and a second algal bloom in the autumn with progressive mixing of nutrients accumulated below the summer pycnocline (Kaiser, 2005). In tidal estuarine environments, mixing may occur throughout the year. Small copepods dominate inshore zooplankton with their seasonal abundance following that of the phytoplankton, and clupeid and scombrid fish are the main consumers of pelagic invertebrates (ibid.).

These broad ocean regions may further be characterised according to ocean processes in different sub-regions. For instance, the North Sea has high species diversity in both zooplankton and fish, and although copepods dominate the zooplankton, euphausiids were found to represent 90% of the plankton biomass in March and April (Williams and Lindley, 1992). Temperature, latitude and season

are important in determining the species composition and abundance of the zooplankton communities (Fransz *et al.*, 1991; Krause *et al.*, 1995; Beaugrand *et al.*, 2001). In contrast, the Norwegian Sea zooplankton is dominated by the herbivorous copepod *Calanus finmarchicus*, which thus provides the dominant link between primary production and higher trophic levels (Aksnes & Blindheim, 1996; Melle *et al.*, 2004). The main predators of *C. finmarchicus* are herring and carnivorous zooplankton species, such as amphipods, medusa and krill (Daewel *et al.*, 2014).

These examples illustrate how plankton assemblages can vary at mid-latitude, continental shelf regions. The abundance of different species that are predators of sea lice larvae and the abundance of other prey will affect the mortality rate of sea lice larvae. Therefore characterising the plankton assemblage at a specific location represents an important step in predicting mortality rate due to predation and incorporating the resulting estimates into sea lice infection models.

5.2 Predator selectivity

The body sizes of predator and prey are fundamental in the study of aquatic food webs (Brooks & Dodson, 1965; Woodward *et al.*, 2005), and their relationship is the subject of ongoing research. Moloney and Field (1991) first postulated that community structure and transfer processes are all size dependent and were the first to develop a size-based model of plankton food webs. Recent attempts at modelling plankton food webs either use empirical rules (Maury *et al.*, 2007; Petchey *et al.*, 2008; Williams *et al.*, 2010), kernel shape functions (*e.g.* Gaussian) (Armstrong, 2003; Troost *et al.*, 2008; Banas, 2011) or Laplacian functions (Fuchs & Franks, 2010). However, Visser & Fiksen (2013) recently proposed basing size-based feeding models on biomechanical and evolutionarily sound principles, such as prey size dependencies and capture probabilities. A 'feeding kernel' represents a description of the probability of prey ingestion given as a function of feeding rate vs. prey size (Figure 2). Feeding kernels are often derived using observations from mono-specific grazing experiments, which only describe the potential to ingest prey of a specific size. In the real world, however, assemblages of prey species mean that true feeding kernels are entirely different, with ingestion patterns in prey assemblages also reflecting aspects of predator behaviour, which explains why some types of food are preferred over others despite size considerations (Wirtz, 2014). Selective grazing in the presence of a broad spectrum of prey size plays an important role in variable feeding relationships (Sommer & Stibor, 2002), and in the case of larval sea lice predation, the abundance of similar-sized prey must be considered as well as the abundance and size selectivity of predators.

Although the relationship between predator and prey body sizes is the primary determinant of grazing selectivity, feeding modes can also affect the size range of plankton selected. Feeding modes can be broadly classified as passive and active ambush feeding, feeding-current feeding and cruise feeding (Kiørboe, 2011), and predators may adjust their feeding behaviour in response to the density of food items, *e.g.* they may swim or wait (Kiørboe & Saiz, 1995; Boenigk & Arndt, 2002), modify the speed of their feeding current (Frost, 1972; Visser *et al.*, 2009) or switch between different feeding modes (Saiz & Kiørboe, 1995). This behavioural plasticity shrinks the overall spectrum of potential prey towards a specific sub-range, and Wirtz (2014) describes two feeding kernels: one for ingestion, which is based on the size range of prey that can be ingested based on biomechanical principles, and one for selection, which describes the actual size range of prey selected according to the availability of prey of various sizes. Despite the variety of feeding modes found in planktonic predators, evidence suggests that the feeding kernels of predators with different feeding modes are similar and have a log-normal shape (Berk *et al.*, 1977; Frost, 1977; Holzman & Genin, 2005). The size range of the ingestion kernel is limited by biomechanical features, whereas the size range of the selection kernel is determined by the behaviour of predators. For example, in filter feeders, morphological features, such as mesh sizes and ciliary distances, determine the size range of accessible prey items, whereas copepods, which have a raptorial feeding mode, harvest distinct size classes (Poulet, 1978; Vanderploeg, 1981; Wirtz, 2014). At high prey densities, many ambush and suspension feeders, such as copepods, typically have a high selectivity resulting in a narrow selection kernel (figure 2a), whereas many facultative, omnivorous feeders, such as jellyfish, typically have broad ingestion and selection kernels (figure 2b) (Wirtz, 2014). High selectivity in copepods as a result of specialisation lowers food availability, but improves performance. Under food scarcity, however, availability becomes more important than performance, and poorly fed predators tend to graze less selectively (DeMott, 1995).

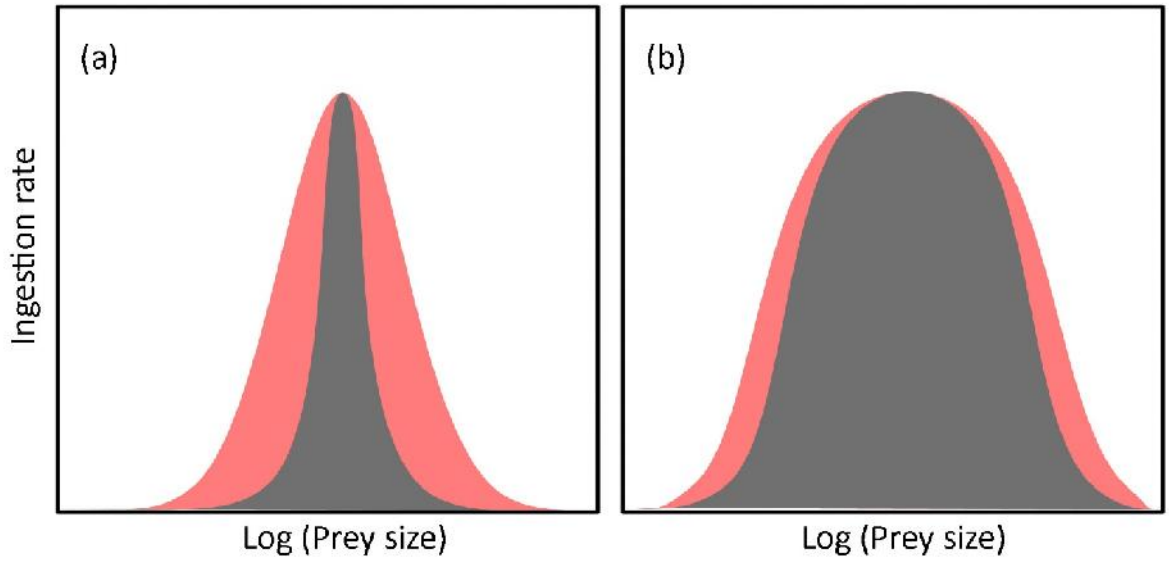

Figure 2. Typical ingestion (red area) and selection (grey area) feeding kernels for (a) narrow-range, selective feeders, *e.g.* copepods, and (b) broad-range, unselective feeders, *e.g.* jellyfish, where prey are abundant. Adapted and redrawn from Wirtz (2014)

5.3 Prey selection

Prey size selection is determined according to the equivalent spherical diameter (ESD), which is the longest axis of the prey, *i.e.* length for sea lice larvae. Johnson and Albright (1991) report that the length of the nauplius I was 0.54 ± 0.04 mm, the nauplius II was 0.56 ± 0.01 mm and the copepodid was 0.70 ± 0.01 mm in *L. salmonis* collected from British Columbian waters. Schram (1993) reports similar ranges from lice collected in Norway.

Potential predators of sea lice larvae are likely to include obligate and facultative carnivorous zooplankton and planktivorous fish, and given their geographical distribution, predators may be represented by chaetognaths, ctenophores, scyphozoa, euphausiids, mysids and scombrid and clupeid fish. In addition, the larval stages of most fish species rely on copepods as their principal dietary component.

Chaetognaths, or arrow worms, are important predators of copepods and are probably major contributors to the structuring of many marine ecosystems (Steele & Frost, 1977). Head width in chaetognaths is a better indicator of prey size selection due to their variable length, and the relationship between head width and prey size generally follows a power curve regression (Pearre, 1980). In *Sagitta elegans*, for example, Rakusa-Suszczewski (1969) reports that individuals collected

from the UK with head widths of ~0.06–1.1mm consumed prey of ~0.03–1.2mm. In *Sagitta enflata*, individuals with head widths of ~0.3–1.1mm consumed prey of ~0.09–0.7mm (Pearre, 1974). Chaetognaths are ambush predators, and Fulton (1984) found that active copepods, such as *Acartia tonsa*, decreased in abundance in the presence of *Sagitta hispida*, whereas inactive swimmers, such as *Oithona* spp. did not as encounter rates were lower. As sea lice larvae are active swimmers, it is likely that they will be predated by chaetognaths.

Ctenophores, or comb jellies, are found throughout the world's oceans, and all are predatory, feeding on zooplankton. A wide range of sizes and body forms exist with several different feeding modes. If food is plentiful, they can eat ten times their own weight per day (Reeve *et al.*, 1978). As an example, the clearance rates of the ctenophore *Mnemiopsis leidyi* at a biomass of 0.2–3 g dry weight m^{-3} were on average 20% of the total prey stock per day in Narragansett Bay, Rhode Island (Deason, 1982). *Pleurobranchia bachei* is a tentaculate ambush entangling ctenophore that primarily preys on copepods. Although it has a broad prey size range, it is highly selective and its feeding profile may be determined according to the relative availability and vulnerability of prey, which in turn can be predicted from prey swimming speeds and susceptibility of prey after encounter (Greene *et al.*, 1986). In laboratory experiments, copepodid I larvae of *Calanus pacificus* with a mean length of 0.74 mm and mean swimming speed of 0.32 mm s^{-1} were most susceptible to predation by *P. bachei*, and later juvenile stages, which are larger, were less susceptible to predation. Adult *C. pacificus* of 2.6–3.0 mm were too large for *P. bachei* (*ibid*.).

Scyphozoa, or jellyfish, are generally larger than many other predators in the plankton, and are seasonally common in many coastal environments including those most commonly employed for marine salmoniculture. Scyphozoa typically range from 2–40 cm, and their stinging or filter-feeding tentacles enable them to ingest various zooplankton taxa of different sizes, including copepods (Purcell, 1992; Purcell *et al.*, 1994; Suchman & Sullivan, 1998). However, research has shown that scyphozoa are highly selective, and prey size has a significant impact on feeding rates (Suchman & Sullivan, 1998, 2000). As scyphozoa are neither visual nor raptorial feeders, they select prey as a consequence of prey vulnerability, and prey with faster swimming speeds and poor escape responses are most vulnerable to predation (Suchman & Sullivan, 2000). For example, feeding rates in the scyphozoan *Chrysaora quinquecirrha* were higher in heat-killed adult *Acartia tonsa* (length = 0.81 ± 0.07 mm and 0.73 ± 0.06 mm for females and males, respectively) than in heat-killed copepodids of the same species (length = 0.55 ± 0.09 mm) (4.9 copepods h^{-1} vs. 0.5 copepods h^{-1}, respectively, at prey densities of 14.3 L^{-1}) (Suchman & Sullivan, 1998). However, adults of *Acartia hudsonica* demonstrated effective escape responses (42–59 mm s^{-1} escape velocity) with respect to the common

scyphozoan *Aurelia aurita*, so that less than 1% of encounters resulted in ingestion, whereas copepodids were more likely to fail to respond and had lower escape velocities (33–39 mm s^{-1}) (Suchman, 2000).

Euphausiid and mysid shrimps are two groups of arthropods that are ubiquitous throughout the world's oceans, and due to their high abundance and position in the food chain, they are important components of marine food chains. While most are filter feeders and feed on phytoplankton and detritus, some are omnivorous and feed on other zooplankton. In the Norwegian Sea, the copepod *Calanus finmarchicus* (which has similar-sized juvenile stages to sea lice) is a dominant prey of euphausiid shrimp. The degree of carnivory in *Meganyctiphanes norvegica* was 40% or less in field studies (Båmstedt & Karlson, 1998), although it is likely that the degree of carnivory is inversely related to the phytoplankton abundance (Stuart & Pillar, 1990), which illustrates the importance of the relative abundance of different prey items in estimating ingestion rates. In the study by Båmstedt & Karlson (1998), average daily rations of copepods were 1–20% of the predator dry weight, corresponding to a reduction in copepod biomass of 0.3–6.4% daily. In other studies, the preferred prey size of *Euphausia hanseni* was 0.39 mm prosome length (Barange *et al.*, 1991) and the preferred prey size of *Nematoscelis megalops* was 0.49 mm (Gibbons *et al.*, 1991).

The larval stages of most fish species rely on copepods as their principal dietary component, and although larger gadoids, such as Atlantic cod (*Gadus morhua*) switch to piscivory as adults, smaller species, such as Norway pout (*Trisopterus esmarkii*) and clupeids, such as herring (*Clupea harengus*) remain planktivorous throughout their lives (Daewel *et al.*, 2014). As larval fish are active raptorial predators and rely on sight to detect prey, active prey may be more susceptible to predation. Tiselius & Jonsson (1990) and Doall *et al.* (1998) suggest that the high turn rates of sea lice copepodids during host-seeking behaviour may make them more attractive to predators, such as fish larvae. Prey size is strongly correlated with the length of fish larvae, and their preferred size range increases as they grow, with the optimum size of prey being 2.8% of larval length in Atlantic herring (*Clupea harengus*) larvae (Munk, 1992).

Some adult fish, such as scombrids and clupeids, feed on plankton throughout their lives, and switch between three feeding modes depending on prey density: particulate feeding on individual prey, gulping where the mouth opens and closes slowly accompanied by slow swimming, and filtering with the mouth agape accompanied by strong swimming (Janssen, 1976). In Atlantic herring, filter feeding and gulping, which are not size-selective and involve the consumption of multiple prey items, were seen when prey densities of *Artemia* spp. were above 50 nauplii L^{-1}, and particulate feeding, which

involves selecting and taking individual prey items, was seen when prey densities were less than 50 nauplii L^{-1} (Gibson & Ezzi, 1985).

Zooplankton consumption by fish in the North Sea has been estimated at 19–25 g C m^{-2} $year^{-1}$ of which 28% of overall zooplankton consumption can be attributed to early life stages of fish (Heath, 2007). In frontal zones, fish larvae could consume up to 3–4% day^{-1} of the fraction of preferred zooplankton sizes (Munk & Nielsen, 1994). Selected values that may give an indication of predator abundance and zooplankton predation for prey of similar sizes to larval sea lice are shown in Table 7.

Table 7. Selected values of predator abundance and zooplankton predation for prey of similar sizes to larval sea lice. For guidance, nauplius I measure ~0.54 mm, nauplius II measure ~0.56 mm and free-living copepodids measure ~0.7 mm (Johnson & Albright, 1991b).

Variable	Value	Reference
Plankton community structure	Species, latitude and season determine zooplankton composition and abundance.	Fransz *et al.*, 1991; Krause *et al.*, 1995; Beaugrand *et al.*, 2001
	Zooplankton abundance follows algal blooms in spring and autumn.	Kaiser, 2005
Prey selection size	Chaetognaths:	
	0.03–1.2 mm	Rakusa-Suszczewski, 1969
	0.09–0.7 mm in *Sagitta enflata*	Pearre, 1974
	Ctenophores:	
	0.74 mm *Calanus pacificus* susceptible to predation by *Pleurobranchia bachei*	Greene *et al.*, 1986
	Scyphozoa:	
	Select vulnerable prey (i.e. slow swimming speed, poor escape response)	Suchman & Sullivan, 2000
	In *Aurelia aurita* <1% of adult *Acartia hudsonica* encountered were ingested. Copepodids with lower escape velocities (33–39 mm s-1) less likely to escape.	Suchman, 2000
	Euphausiids and mysids:	
	0.39 mm prosome length in *Euphausia hanseni*	Barange *et al.*, 1991
	0.49 mm in *Nematoscelis megalops*	Gibbons *et al.*, 1991

	Fish:	
	Prey size strongly correlated with length of fish larvae. Optimum prey size 2.8% of larval length in Atlantic herring (*Clupea harengus*).	(Munk, 1992)
Clearance rate	20% of the total prey stock per day in ctenophore *Mnemiopsis leidyi* at biomass of 0.2–3 g dry weight m^{-3}	Deason, 1982
	0.3–6.4% copepod biomass consumed daily (1–20% euphausiid predator dry weight)	Båmstedt & Karlson, 1998
	In North Sea, zooplankton consumption by fish estimated at 19–25 g C m^{-2} $year^{-1}$ (28% attributed to larval fish).	Heath, 2007
	In frontal zones, fish larvae may consume 3–4% day-1 of preferred zooplankton sizes.	Munk & Nielsen, 1994

In addition to planktonic predators, sessile feeders, particularly bivalve molluscs and cnidarians, could also have potential impact on larval sea louse survival. Bivalve molluscs, specifically the blue mussel *Mytilis edulis*, have been suggested to provide efficient clearance of mesoplankton of the same size order as sea lice larvae, with medium sized mussels suggested to be able to process 24 L day^{-1} (Davenport *et al*. 2000) and to provide ~90% clearance of *Artemia* nauplii (~300 µm) and ~34% clearance of the free-swimming copepod *Tigriopus brevicornis* (1.0-1.2 µm) in feeding experiments. Only blue mussels and scallops (*Placopecten magellanicus*) have been specifically investigated in terms of their ability to clear larval sea lice (Molloy *et al*. 2011, Bartsch *et al*. 2013). Molloy *et al*. (2011) demonstrated that mussels were capable of removing copepodids from the water column under experimental conditions and this was also demonstrated by Bartsch *et al*. (2013) who showed that mussels and scallops could remove 18-38% of presented copepodids per hour. While it has been suggested that mussels or other bivalves might therefore be employed to help control sea lice on farms (Molloy *et al*. 2011, Bartsch *et al*. 2013), it has been noted (Sandra Bravo, pers. comm.) that close proximity of mussel farms and salmon farms in Chile has not served to reduce apparent levels of sea louse infection.

6 Research gaps identified, recommendations and conclusions

A broad range of factors impact the levels of egg production by host-attached lice and the subsequent proportion of the initial extruded egg number that go on to successfully infect fish as copepodid larvae. Some of the key factors explored in this review are listed in Table 8, although there are extensive interactions / overlaps between many of these factors *e.g*. season, light temperature and salinity. Figure 3 shows the stages of the sea louse life cycle that determine the number of copepodids available for infection and their infection success and summarises the factors reviewed in this study that may affect subsequent levels of infection.

Table 8. Biotic and abiotic factors affecting the number of successfully infecting copepodids. Words in italics are key factors that require further investigation.

Environmental Factors	**Louse biology**	**Host Biology**	**Other factors**
Season	Louse genetics	Host history	Dispersive losses
Light	Louse disease	Host genetics	Encounter rate
Temperature	*Egg Production*	Stocking density	
Salinity	*Hatching success*	Host susceptibility	
Pressure (depth)	Stage Development	Host size/age	
Wind	*Predation*		
Current	*Infectivity profile*		
Density gradients			
Tidal cycle			

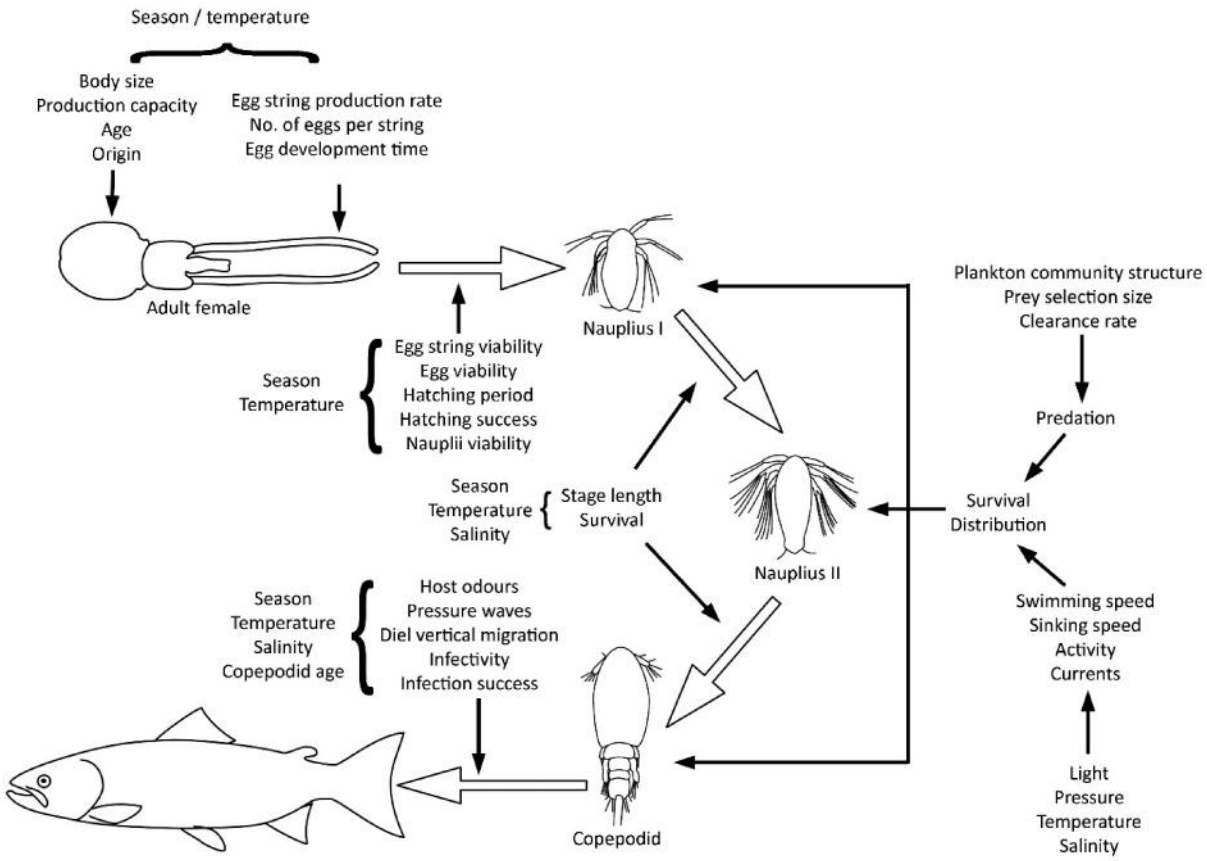

Figure 3. A conceptual model of the stages of the sea louse life cycle that determine the number of copepodids available for infection and their infection success, with factors that may affect survival / infectivity at each stage. Open arrows show the life cycle and black arrows show the factors that may affect each stage of the life cycle.

A simplified conceptual framework can be employed to summarise the findings of this review, which describes the relationships between the production and loss of free-swimming larval lice and aspects of their behaviour that together determine subsequent infection levels:

$$\boldsymbol{S} = \quad P - M \quad * I$$

Where *S* = Number of successfully infecting copepodids, P = Production (*i.e*. egg number, egg viability and egg hatching success) M = Mortality of free-living stages (*i.e*. impact of predation, disease and senescence) and I = Infectivity (*i.e.* capacity of individual copepodids to infect hosts and the occurrence of opportunities to infect). The operational use of this conceptualised framework requires the estimation of the components of each of these variables, which are themselves influenced by a range of biotic and abiotic factors.

By forming a table of these variables and the observable factors that may influence them (Table 9.), it is clear that there are a considerable number of permutations, each requiring observational data to allow variables to be fully defined. While a number of these variables have been previously investigated, as described in this review, a lack of data for some variables results in an incomplete dataset (Table 9). Furthermore, a lack of standardisation and consistency across different studies due to various experimental conditions and the origin of experimental lice, *e.g*. Atlantic or Pacific strains, farmed or wild origin, cold-adapted or not, means that many data points are not directly comparable. In addition, some studies are based on laboratory experiments conducted under controlled conditions, whereas others are based on field data. Gravil (1996) recorded the widths of nauplius I larvae and the lipid reserves from field-collected lice at different times of year, and although no other studies considered seasonal variations in their experiments *per se* (Table 9), seasonal variation subsumes a number of observable / observed factors, such as temperature, photoperiod and salinity, and other factors that are not considered here, such as host condition and plankton assemblages.

6.1 Key gaps in knowledge identified

There are a very great number of gaps in our knowledge concerning the variables affecting levels of sea louse infections. Some variables, however, are likely to have both a greater proportional / numerical impact and to be more tractable to parameterisation by experimental means. These are addressed below.

6.1.1 Egg production, egg viability and hatching success

Previous estimates of egg production in the literature vary across more than an order of magnitude, are relatively inconsistent and are incomplete in their coverage of relevant factors. As this is the key input variable driving subsequent modelled infection levels, better estimates of production are an obvious priority. In addition to this, it is clear from the relatively sparse earlier studies that have been conducted that egg viability and hatching success are rarely, if ever 100% and can be substantially lower than this according to a range of factors (Table 2).

Table 9. A summary table of parameters influencing the production, timing and survival of sea lice larvae and observable biotic and abiotic factors that may influence them. Cells marked with an X represent areas where some data already exist and blank cells represent areas of data deficiency.

	Variable factor					
Parameter	**Origin: Wild / Farmed**	**Temp.**	**Salinity**	**Light / Photoperiod**	**Season**	**Reference**
Female size	X	X		X		Heuch *et al* ., 2000; Tully & Whelan, 1993; Gravil, 1996
Egg string production rate		X				Heuch *et al* ., 2000
No. of eggs	X	X		X		Heuch at al., 2000; Ritchie *et al* ., 1993; Johnson & Albright, 1991a; Gravil, 1996; Tully, 1992
Egg development time		X				Johnson & Albright, 1991a; Johannessen, 1978; Boxaspen, 2000
Hatching period		X	X			Johnson & Albright, 1991a; Gravil, 1996
Egg viability		X	X	X		Johnson & Albright, 1991a; Heuch, 2000; Gravil, 1996
Hatching success		X	X	X		Johnson & Albright, 1991a; Gravil, 1996
Nauplius I development time		X				Johnson & Albright, 1991a; Boxaspen and Naess, 2000; Wootten *et al* ., 1982; Johannessen, 1978; Gravil, 1996
Nauplius II development time		X				Johnson & Albright, 1991a; Boxaspen and Naess, 2000; Wootten *et al* ., 1982; Johannessen, 1978
Nauplius I width					X	Gravil, 1996
Nauplius I lipid reserve width					X	Gravil, 1996
Survival to copepodid		X	X			Johnson & Albright, 1991a; Gravil, 1996
Copepodid survival time		X	X			Johnson & Albright, 1991a; Gravil, 1996

Egg production level is influenced by a broad range of factors including temperature (and temperature adaptation), salinity, host state (nutrition, immunity, stress, genotype), egg batch and others. For this reason, it will be extremely difficult to establish realistic values through tightly controlled laboratory experiments alone. Egg production can, however, easily be established through a programme of farm sampling over a year, with counts of eggs per millimetre and the measurement of egg string lengths being conducted on-farm using a stereomicroscope or in the laboratory following sample preservation. Laboratory analysis could also employ image analysis to increase accuracy and sample throughput. During the sampling period, the recording of farm metadata, such as temperature, salinity, salmon stock, feed source, treatment regime *etc*., would allow an accurate and informative predictive model to be produced. In order to give a better picture of total egg production, samples from wild salmonids would also be helpful as it is well-recognised that egg strings sourced from lice on wild fish tend to have higher numbers of eggs.

Laboratory experiments could investigate controllable factors, *e.g.* using a range of temperatures and salinities, ideally for lice sampled from different ambient temperatures, *e.g*. winter, spring, and summer.

The viability of eggs and hatching success are key mediators of the final number of released larvae. These parameters can be obtained by examining and hatching egg strings from challenges and / or farm samples under controlled conditions of temperature and salinity.

6.1.2 Predation in plankton

The level of predation of larval sea lice in the plankton remains unknown. However, it is clear from other plankton studies that losses to predation are likely to be substantial. In addition, the level of predation will vary according to season, local weather conditions and the composition of the plankton assemblage at any given time. Knowledge of predation levels will not only facilitate more accurate modelling of infection levels but could also guide co-ordinated treatment strategies at particular times of year.

Even with good estimates of larval production, the fate of larvae in the plankton is a key mediator of numbers available to infect fish. Plankton studies are notoriously difficult and are not easily amenable to laboratory-based experiments. To achieve estimates of mortality in plankton, mesocosm studies offer the best approach, whereby in different seasons local plankton are enclosed in a mesocosm and a known number of larval sea lice introduced to the system. Following a period to allow for predation,

the filtering of the mesocosm will allow estimations of plankton types/species present and the clearance rates of sea louse larvae. The use of molecular tools might also allow an investigation of the major predators in any given plankton sample.

Using the same system with introduced “sentinel” salmonids, one could also establish the resulting infection levels, which, while not wholly realistic, would allow some estimation of both the effects of predation and also encounter rate on infection success.

6.1.3 Infectivity profile

There has been a tendency up to the present day, to equate the number of copepodids in the water column with the number of infecting individuals. From previous observations, it is, however, apparent that there is a profile of infectivity (the ability of lice encountering a fish to infect it as they age), with newly moulted individuals being less infective than those having matured for 1–2 days and a subsequent decline of infectivity towards death. Even under the optimal conditions of an experimental infection challenge, the infective success of maximally infective copepodids is rarely higher than 50% and is frequently lower. From the literature, few researchers have attempted to establish infection profiles for cohorts of copepodids under different conditions of, for example, temperature, salinity and current speed, despite clear evidence that these factors will all affect infection success. Most challenge experiments employ static tanks and long exposure times, providing a totally inaccurate reflection of probabilities for real-world infection success.

The infectivity profile needs to be fully established under laboratory conditions. These will not fully reflect field conditions but will tend to provide an overestimate of infection success rate. Using standard tank challenges it would be possible to profile the infectivity of copepodids with age and under different temperature and salinity conditions. A more accurate reflection of infectivity may be achieved using flume experiments where fish are exposed to copepodids under current flow conditions more reflective of field conditions.

One important source of potentially valuable data concerning losses entailed between egg hatching and reinfection of hosts, comprises the detailed farm louse counts already conducted in many countries. Assuming knowledge of seasonal levels of egg production / viability, which may be easily obtained, the annual profile of copepodid / chalimus counts can provide an indication of the proportion of hatched larvae that successfully re-establish infections on fish.

6.2 Co-ordinated research

In order to obtain the greatest benefits from modelling studies, the gaps identified need to be filled for lice and environments in all the regions experiencing problems with *L. salmonis* and independently for other species *e.g*. *C. rogercresseyi*. This means co-ordinating international efforts to ensure that studies are inter-comparable, and this would ideally be achieved through international agreements for matched funding by key national industry and government funders.

6.3 Conclusions

The estimation of lice burdens on wild and cultured fish can inform the timing of pest management decisions in salmonid aquaculture. In the life cycle of the sea louse, egg-production and the survival of the free-swimming stages are key determinants of the numbers of lice available for infection. Despite several decades of research, however, knowledge of this area of sea louse biology is lacking, which confounds the accurate estimation of lice infections using epidemiological modelling. Even where parameters have been measured by researchers, the wide variety of data sources and experimental approaches employed limits the possibility of providing "best" or consensus values for use in modelling. With further research of the key variables that affect the production and survival of free-swimming larval sea lice, it should be possible to more accurately model the production and dispersal of lice from cage aquaculture and wild fish, which will inform the optimum timing of pest management procedures. Furthermore, with an improved knowledge of larval sea louse mortality, it may be possible to incorporate natural processes into management decisions and time treatments appropriately, *e.g*. reflecting larval predation following spring algal blooms. While many aspects of louse biology are important in determining the numbers of lice available for infection, care should be taken to avoid the over-parameterisation of sea louse infection models. The identification of the key variables from the complex biology of sea lice that have the greatest impact on their numbers can be achieved through a sensitivity analysis of model parameters. Accurate predictions of sea lice infections are a single component of integrated pest management protocols, and when used in conjunction with the continuous monitoring of lice populations on farmed fish and effective treatment procedures, it should be possible to minimise the environmental and economic impact of these pathogens on farmed and wild salmonids.

6.4 Draft publications arising from this project

1. Production, mortality and infectivity of larval sea lice, *Lepeophtheirus salmonis* (Krøyer, 1837): current knowledge and implications for epidemiological modelling.

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SARF - Member Organisations

Industry

SEAFISH
Association of Scottish Shellfish Growers
Scottish Salmon SSPO
British Trout Association

Government and Regulators

Scottish Natural Heritage
SEPA Scottish Environment Protection Agency
marinescotland
The Scottish Government
HIE Highlands and Islands Enterprise
Iomairt na Gaidhealtachd 's nan Eilean

Non-Governmental Organisations

The Crown Estate
Scottish Environment LINK
Rivers & Fisheries Trusts of Scotland
Safeguarding Scotland's Rivers & Lochs
ASFB The Association of Salmon Fishery Boards