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Review Article

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

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Current sea louse models attempt to estimate louse burdens on wild and cultured salmon by predicting the production and distribution of lice larvae and estimating the risk of transmission. While physical characteristics of water bodies and weather can be accurately modelled, many aspects of sea lice biology require further parameterization. The aims of this review are (i) to describe current knowledge regarding the production, mortality, and infectivity of planktonic sea lice larvae and (ii) to identify gaps in knowledge and suggest research approaches to filling them. Several major gaps are identified, and those likely to have the greatest impact on infection levels are (i) egg production, viability and hatching success, (ii) predation in plankton and (iii) copepodid infectivity profiles. A key problem identified in current parameter estimates is that they originate from a number of sources and have been determined using a variety of experimental approaches. This is a barrier to the provision of "best" or consensus estimates for use in modelling. Additional and more consistent data collection and experimentation will help to fill these gaps. Furthermore, coordinated international efforts are required to generate a more complete picture of sea louse infections across all regions experiencing problems with sea lice.

Keywords: Atlantic salmon, epidemiology, *Lepeophtheirus salmonis*, modelling, sea lice

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.), whereas in the North Pacific, *Lepeophtheirus salmonis oncorhynchii* (Johnson and Albright, 1991a) is prevalent in cultured salmon, although *Caligus elongatus* von Nordmann, 1832 also has some impact. In the southern hemisphere *Caligus rogercresseyi* Boxshall and Bravo 2000 is the principal pathogenic species affecting the Chilean salmon aquaculture industry. For the Norwegian salmon industry, where costs are best characterized, the economic impact of sea lice was estimated to be in excess of 3.4 billion NOK per annum (>£300M) in 2014 for 1 272 358 tonnes production (Iversen *et al.*, 2015) with costs estimated to exceed 5 billion NOK (>£390M) in 2015 for 1 303 346 tonnes = 3836.28 NOK tonne^{-1} (Audun Iversen, pers. comm.). Higher estimates of 7–8 billion NOK per annum (>£540M) have also been presented (Rødseth, 2016). Using FAO statistics for global cultured Atlantic salmon production in 2015 (http://www.fao.org/fishery/statistics/global-aquaculture-production/en) for all countries that experience sea

lice problems (2 332 290 tonnes) and Iversen's estimate of cost per tonne for 2015 (3836.28 × 2 332 290) provides a rough cost estimate of ∼9 billion NOK globally for 2015 (∼£700M), with costs likely to have continued to rise since then.

Current integrated pest management (IPM) strategies for sea lice control rely on a small number of licensed pesticides, few of which are effective against all stages of the parasite's life cycle, combined with effective husbandry management tools, such as single-cohort stocking, optimized stocking densities, the use of cleaner fish in polyculture, and fallow periods (Leclercq *et al.*, 2013; Skiftesvik *et al.*, 2013). Physical techniques to exclude lice, such as the use of barrier nets and snorkel cages, coupled with mechanical tools, including thermal and turbulent de-licers and laser removal, also constitute an increasing component of current IPM strategies. The adoption of such an increasingly multimodal approach means that the timing of management decisions is critical to the successful control of the parasite. A central element required for the prediction of fluxes in lice populations is an understanding of the production, survival, dispersal, development, and infectivity profile 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 10 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. Although complex physical coastal processes can now be reasonably 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 characterized by small body sizes, high fecundities, and short generation times. Although offspring of r-strategists are dispersed widely, they have a low probability of survival (Cavaleiro and Santos, 2014). However, sea lice differ from many other r-strategists in that they are attached to a host, which provides a permanent food source and allows anomalies, such as a larger body size, and raises the question of whether they have a high fecundity because they experience heavy losses during the larval stages or because they have a nominally unlimited food source. The high fecundity and wide larval dispersal are key aspects of the sea louse's life cycle that determine its overall survival and success. As a result, fecundity and larval biology 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. Once a copepodid has attached to a host, development is more predictable as development after infection is unaffected by copepodid age at infection (Tucker *et al.*, 2000a; Pedersen, 2009), although at this point host factors such as host species/genotype, immunity, and site of infection intervene to affect success. Transmission is still a contentious issue with disagreement over whether lice (despite water currents) are accumulated at their source (e.g. Krkošek *et al.*, 2005 and implied by Jansen *et al.*, 2012) or hydrodynamically spread over large distances (e.g. Brooks, 2005; Asplin *et al.*, 2014). Therefore, accurate data are urgently needed to inform and validate increasingly 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 and Mo, 2001; Murray, 2002; Tucker *et al.*, 2002). 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 and exogenous sources of mortality, such as predation.

Particle tracking models predict the dispersal over time of particles generated at a point source using hydrodynamic models (e.g. Corner *et al.*, 2006), which calculate local current velocities based on local topography, fluid dynamics, and external forcing from tidal elevation, freshwater inputs, and wind-generated currents. 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 100 km in just a few days (Asplin *et al.*, 2004).

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.

More recent models have become increasingly complex, and Asplin *et al.* (2011, 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. In addition, a recent model similar to the one utilized 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).

Aldrin *et al.* (2013) and Kristoffersen *et al.* (2014) present a model based on a statistical network of Norwegian salmon farms. Monthly external and internal infection pressure and the risk of infection between neighbouring farms are predicted based on lice burden estimates from the previous month and the distances between neighbouring farms. The model is fitted to actual lice

counts from Norwegian farms between 2003 and 2011. It uses temperature-dependent fecundity and larval demographics, although mortality rates for free-swimming larvae and chalimus stages are fixed.

While these 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 Sandvik 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. Aldrin *et al.*, 2013; Johnsen *et al.*, 2014) or vary according to salinity (e.g. Amundrud and Murray, 2009; Adams *et al.*, 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 parameterization 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 considered sufficiently developed to warrant their use as components of an integrated sea louse management strategy. For example, Norwegian salmon farming from 2017 will be regulated regionally through an operational management system comprising the application of predictive models that predict louse infection intensities along the entire coastline (Asplin *et al.*, 2014), combined with a process of continuous model validation and calibration against real-world data (Bjørn *et al.*, 2014; Sandvik *et al.*, 2016).

The aims of this review and analysis were as follows:

(1) To analyse the available literature to determine current knowledge regarding the recruitment and survival of free-swimming nauplii and copepodid larvae and factors that affect the longevity and infectivity of copepodids. Where no specific data regarding sea lice were available, the wider literature was 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.

Additional considerations:

- While this review focuses primarily on *Lepeophtheirus salmonis* spp., observations from other species that are problematic in salmonid aquaculture are also noted where appropriate.
- This review also focuses principally on knowledge concerning louse larvae deriving from farmed fish due to both their greater accessibility and the fact that environmental parameters can only be sufficiently controlled or consistently measured in defined water masses.
- Hitherto, there has been some conflation of data arising from Atlantic and Pacific sea louse studies. Evidence for clear genomic and phenotypic differences between these subspecies has made it evident that the origin of data regarding these subspecies should be considered when interpreting the results.

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.

Fecundity

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. Koop and Field, 1980; Williams, 1985; Johnston and Dykeman, 1987; Maranhão and Marques, 2003). Similarly, 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 and Whelan, 1993). Heuch *et al.* (2000) found that adult female lice of wild origin in Norway were significantly larger than 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 and Whelan, 1993). A similar pattern was reported 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 at an average of 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 under experimental conditions (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 (1991b) 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

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

	L. salmonis salmonis			*L. salmonis oncorhynchi*		
	Time (d)	**Egg string pairs**	**No. of eggs**	**Time (d)**	**Egg string pairs**	**No. of eggs**
Egg string production rate						
7.2°C	11[a]	–	–	nd	–	–
12.2°C	5[a]	–	–	nd	–	–
Production capacity	–	4.95[a]	–	–	nd	–
No. egg strings per string						
7.2°C	–	–	First string 152 subsequent strings 285[a]	–	–	nd
10°C	–	–	nd	–	–	344.6 ± 79.8[b]
Firt string	–	–	141.09 ± 22.19[c]	–	–	nd
Second string	–	–	216.4 ± 67.59[c]	–	–	nd
Third string	–	–	208.2 ± 50.97[c]	–	–	nd
Wild lice	–	–	965 ± 30.1[d]	–	–	nd
Farmed untreated lice	–	–	758 ± 39.4[d]	–	–	nd
Farmed treated lice	–	–	297 ± 19.1[d]	–	–	nd

References: (a) Heuch *et al.* (2000), (b) Johnson and Albright (1991b), (c) Gravil (1996), (d) Pike and Wadsworth (1999), nd = no data available.

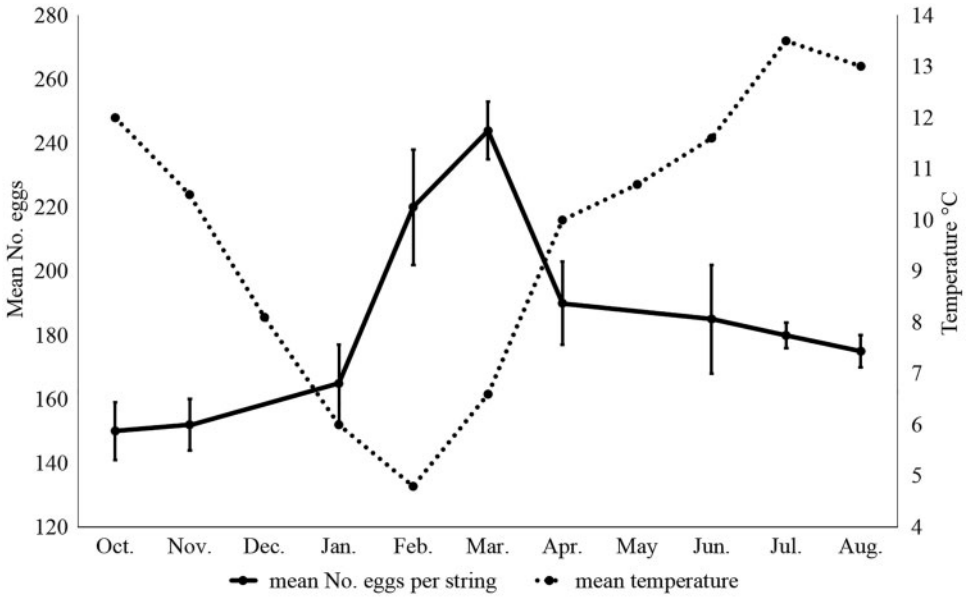

Figure 1. Relationship between water temperature and the number of eggs per egg string in *Lepeophtheirus salmonis* from salmon farms on the West Coast of Scotland. Redrawn from Ritchie *et al.* (1993).

egg strings. It appears that there may be a difference in the batch size in Atlantic *L. salmonis salmonis* (Heuch *et al.*, 2000; Gravil, 1996) and the Pacific *L. salmonis oncorhynchi* (Johnson and Albright, 1991a), which highlights the importance of discriminating between the two subspecies (Skern-Mauritzen *et al.*, 2014). 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.

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 lag may reflect the time required for egg strings to develop before being extruded at low temperatures. Samsing *et al.* (2016) found a similar trend in lice acclimatized in the laboratory at different temperatures with the number of eggs per string increasing from ∼135 ± 5 at 20°C to ∼295 ± 10 at 5°C. In the same experiment, it was found that the number of eggs per string produced at 3°C was lower (∼153 ± 10) than at the higher temperatures tested. This decrease corresponded to a decreased body size and coincided with a

Table 2. Key values of hatching in *L. salmonis*.

	L. salmonis salmonis		*L. salmonis oncorhynchi*	
	Proportion	**Time (h)**	**Proportion**	**Time (h)**
Non-viable egg strings	2.41%[a]	–	nd	–
Non-viable eggs per string	17.66%[a]	–	nd	–
7.2°C	13.3%[b]	–	nd	–
12.2°C	7.5%[b]	–	nd	–
Hatching period				
5°C	–	240[a]	–	nd
7°C	–	192[a]	–	nd
10°C	–	144[a]	–	31.7 ± 17[c]
Hatching success at 10°C				
0 ppt	3.27%[a]	–	nd	–
10 ppt	nd	–	0%[c]	–
15 ppt	nd	–	70%[c]	–
20 ppt	nd	–	78%[c]	–
25 ppt	nd	–	100%[c]	–
30 ppt	86.36%[a]	–	nd	–
Hatching success at 34 ppt				
3°C	28 ± 4%[d]	–	nd	–
5°C	85 ± 4%[d]	–	nd	–
7°C	90 ± 4%[d]	–	nd	–
10°C	87 ± 3%[d]	–	nd	–
15°C	100%[d]	–	nd	–
20°C	100%[d]	–	nd	–
Viability of nauplii				
20 ppt	nd	–	19.8% (0–89.9)	–
25 ppt	nd	–	51.1% (12–94.1)	–
30 ppt	nd	–	65.9% (9.7–95)	–

References: (a) Gravil (1996), (b) Heuch *et al.* (2000), (c) Johnson and Albright (1991b), (d) Samsing *et al.* (2016), Mean ± *SD*, parentheses indicate ranges, nd = no data available.

failure in larval development, and it was speculated that this temperature could be close to the limit of their biological tolerance, at least for the tested lice (Samsing *et al.*, 2016).

A variety of other factors may also affect lice fecundity. As an example, host condition and the use of chemotherapeutants have been proposed as possible influences on egg string length and the viability of larvae (Tully and Whelan, 1993). Likewise, fecundity may vary with host species, either as a result of diet, the physiological status of the fish, or genetic variation (Johnson and Albright, 1992; MacKinnon *et al.*, 1995; MacKinnon, 1998). This follows from the intimate metabolic associations between hosts and parasites, which are often reflected in the evolution of their genomes (e.g. Zarowiecki and Berriman, 2015). It has also been suggested that host immune responses may modify lice fecundity. For instance, Grayson *et al.* (1995) found that gravid female lice on Atlantic salmon injected with extracts derived from adult *L. salmonis* had a significantly lower fecundity than control fish. Similarly, Nilsen (2016) has presented work suggesting that use of a recombinant vaccine to the salmon louse Ls4D8 protein, a homologue to subolesin in ticks and my32 in *C. rogercresseyi*, gave rise to reduction in egg strings. Host-related and abiotic conditions may not be the only factors governing salmon louse fecundity. As an example, intraspecific competition between lice on a given host is suggested to result in reduced fecundity with increasing salmon louse infection densities (Ugelvik *et al.*, 2017). Louse fecundity is clearly the product of a number of biotic and abiotic factors, most of which remain to be fully characterized.

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. Similarly, Samsing *et al.* (2016) found that hatching success was strongly influenced by water temperature, with 100% success at 20°C and 15°C decreasing to 28 ± 4% success at 3°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 1 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).

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 (1991b) 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 3. Key stage timings for *L. salmonis* (mean values).

	L. salmonis salmonis		*L. salmonis oncorhynchi*	
	Time (d)	**Time (h)**	**Time (d)**	**Time (h)**
Egg development time				
2°C	45.1 ± 0.5[e]	–	nd	–
3°C	35.2 ± 0.4[e]20.8 ± 1.5[f]	–	nd	–
4°C	27.6 ± 0.2[e]	–	nd	–
5°C	21.6 ± 0.1[e]13.0 ± 7.8[f]	–	17.5[a]	–
9°C	33–39[b]	–	nd	–
9.5°C	25[b]	–	nd	–
10°C	8.7 ± 0.1[e]4.6 ± 1.3[f]	–	8.6[a]	–
11.5°C	10–14[b]	–	nd	–
15°C	2.88 ± 1.0[f]	–	5.5[a]	–
20°C	1.8 ± 0.5[f]	–	nd	–
Duration of first nauplius stage				
5°C	–	nd	–	52[a]
7.5°C	–	43.25[d]	–	nd
9.2°C	–	35[b]	–	nd
10°C	–	nd	–	30.5[a]
12°C	–	18[c]	–	nd
15°C	–	nd	–	9.2[a]
15.5°C	–	12[b]	–	nd
Duration of second nauplius stage				
5°C	–	nd	–	170.3[a]
9.2°C	–	77[b]	–	nd
10°C	–	nd	–	56.9[a]
11°C	–	63[bc]	–	nd
12°C	–	46[c]	–	nd
15°C	–	nd	–	35.6[a]
19°C	–	33[c]	–	nd
Development time to copepodid				
2°C	–	1644[e]	–	nd
5°C	–	276[f]	–	nd
7°C	–	168[f]	–	nd
10°C	–	111–177.5[d]305[e]108[f]	–	nd
15°C	–	36[f]	–	nd
20°C	–	48[f]	–	nd

References: (a) Johnson and Albright (1991b), (b) Johannessen (1977), (c) Wootten et al. (1982), (d) Gravil (1996), (e) Boxaspen and Næss (2000), (f) Samsing *et al.* (2016), nd = no data available.

The hatching period is variable, and Johnson and Albright (1991b) 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 based on personal observations, although this may represent a difference between Atlantic and Pacific *L. salmonis*.

Stage timings

Development times are highly dependent on temperature and have been addressed in various studies summarised in Table 3. Overall, the egg development time varies between 1.8 and 45.1 days for temperatures ranging between 2 and 20°C (Johnson and Albright, 1991b, Boxaspen and Næss, 2000; Samsing *et al.*, 2016). The duration of the first nauplius stage varies between 9.2 and 52 h at temperatures ranging between 5 and 15°C, while the corresponding duration for the second nauplius stage varies between 33 and 170.3 h for temperatures ranging between 5 and 19°C (Johannessen, 1977; Wootten *et al.*, 1982; Johnson and Albright, 1991b, Gravil, 1996). Durations of the stages seem to be comparable for Pacific and Atlantic lice, and reported ranges agree with the ranges found in publications where developmental times were reported for both naupliar stages combined (Gravil, 1996; Boxaspen and Næss, 2000; Samsing *et al.*, 2016). 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).

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 min and 12.21 ± 3.87 min, 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 and 11°C, whereas acclimation at 11.5°C allowed larval development up to 22°C. In adult lice maintained at 3°C, however, nauplii failed to develop to copepodids (Samsing *et al.*, 2016).

Survival

Nauplii that hatch successfully are planktonic. At this stage they do not feed, but are lecithotrophic (yolk feeding) and rely on their energy reserves until they moult to infective copepodids and find a suitable host (Johnson and Albright, 1991b). 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 or compensate for a higher temperature-dependent metabolism of the non-feeding larval stages, although no data are available comparing survival at different times of year.

Johnson and Albright (1991b) 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 to 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. Samsing *et al.* (2016) found that sea lice larvae from Scotland did not proceed past the nauplius II stage at 5°C and 3°C, respectively, but died before moulting to copepodids, and at 7.5°C, very few copepodids were obtained (Gravil, 1996). 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 1 day (Johnson and Albright, 1991b). 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 and Fyhn, 1985; Pike and 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 also 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 (1991b) report that survival was prolonged at salinities of 15–30‰ and temperatures of 5–15°C, and that mean survival times were between 2 and 8 days. Similarly, Wootten *et al.* (1982) report that the mean survival time of copepodids at 12°C was 4 days at an unspecified salinity. 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 (1991b), 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 and Albright, 1991b), and survival is severely compromised at salinities below 29‰ (Tucker *et al.*, 2000b). 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 and Fyhn, 1985) and these authors suggest that, unlike adult lice, the 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 these are feeding stages, some protection would be received from ingested host tissue.

The survival time of copepodids is inversely related to temperature, and Samsing *et al.* (2016) report that the survival time of 80% of copepodids was 12.5 days at 7°C, 13 days at 10°C, 9.5 days at 15°C, and 6 days at 20°C; at 5°C it was reduced to 10 days. This pattern is presumably due to lower metabolism and, therefore, increased longevity of energy reserves at lower temperatures, although at very low temperatures there appear to be other factors limiting survival. Median survival times reported by Gravil (1996) were 116 h at 5°C, 90 h at 10°C, and 82 h at 15°C at full salinity (35‰), although these appear to be gross underestimations and may be due to sub-optimal culture conditions. 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 (Gravil, 1996). 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.

Behaviour

While both of the free-swimming larval stages are planktonic, the nauplius stages of sea lice are principally dispersal stages, whereas the copepodid stage must locate, re-establish contact with, and subsequently infect a suitable host. The larvae are subject to currents, which serve to disperse them over a wide area, and although the larvae have limited movement capabilities, their dispersal can be partially influenced by certain behaviours, e.g. aggregating at particular depths in the water column

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

	L. salmonis salmonis			*L. salmonis oncorhynchi*		
	Width (μm)	**Proportion**	**Time (h)**	**Width (μm)**	**Proportion**	**Time (h)**
Nauplius I width						
May	187.76[a]	–	–	nd	–	–
August	214.05[a]	–	–	nd	–	–
Nauplius I lipid reserve width						
May	112.98[a]	–	–	nd	–	–
August	135.84[a]	–	–	nd	–	–
Survival to copepodid at 10°C						
<25 ppt	–	0%[a]	–	–	nd	–
<30 ppt	–	nd	–	–	0%[b]	–
30 ppt	–	nd	–	–	35.2%[b]	–
35 ppt	–	18.33%[a]	–	–	nd	–
Copepodid survival time at 10°C						
0-10 ppt	–	–	15[a]	–	–	nd
5 ppt	–	–	nd	–	–	3[b]
10 ppt	–	–	nd	–	–	<24[b]
15 ppt	–	–	54[a]	–	–	nd
16 ppt	–	–	4[c]	–	–	nd
19 ppt	–	–	6[c]	–	–	nd
20 ppt	–	–	67[a]	–	–	nd
23 ppt	–	–	8[c]	–	–	nd
25 ppt	–	–	68[a]	–	–	Max. 17d[b]
26 ppt	–	–	11[c]	–	–	nd
29 ppt	–	–	24[c]	–	–	nd
30 ppt	–	–	55[a]	–	–	nd
33 ppt	–	–	22[c]	–	–	nd
35 ppt	–	–	64 (max. 18d)[a]	–	–	nd
36 ppt	–	–	25[c]	–	–	nd
Copepodid survival time at 35 ppt						
5°C	–	–	116[a] 240 (LT_{80})[e]	–	–	nd
7°C	–	–	300 (LT_{80})[e]	–	–	nd
10°C	–	–	90[a] 312 (LT_{80})[e]	–	–	nd
12°C	–	–	96[d]	–	–	nd
15°C	–	–	82[a] 228 (LT_{80})[e]	–	–	nd
20°C	–	–	144 (LT_{80})[e]	–	–	nd

References: (a) Gravil (1996), (b) Johnson and Albright (1991b), (c) Bricknell *et al.* (2006), (d) Wootten et al. (1982), (e) Samsing *et al.* (2016), nd = no data available.

(Johnsen *et al.*, 2014). In order to maximize 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 behavioural responses can be categorized 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 include light, chemical, pressure, temperature, and water flow/vibration.

Swimming speed/activity

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 for the lecithotrophic larvae of *L. salmonis*, which must conserve their limited energy reserves wherever possible. Despite their energy considerations, copepodids must maintain their position in the water column where their chances of encountering hosts are highest (Bron, 1993). However, Gravil (1996) found the activity of nauplii and copepodids to be 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. However, these results may be affected by insufficient acclimation.

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 a speed of 2 cm s^{-1} was sustained when stimulated. In comparison, the reported swimming speed of salmon is of two orders of magnitude higher (Colavecchia *et al.*, 1998). Thus, while chemotaxis may be important in positioning the larvae in suitable water masses, the pursuit of a salmon host, as opposed to the interception of it at close range, is not a viable strategy.

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 speeds 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 in turn 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 (Bron *et al.*, 1993). 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 (2014) observed declining number of attaching copepodids with increasing current speed. Following a dose of 2500 copepodids $fish^{-1}$ introduced 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 (2014) has 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.

Light

Copepodids of *L. salmonis* are highly photopositive and move toward 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 (Gravil, 1996). The free-swimming larval stages of *C. elongatus* are also phototactic, with the copepodids showing a contrasting greater response to light than the nauplii stages (Hogans and Trudeau, 1989). In *L. salmonis*, a peak response was seen at a wavelength 500 nm 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 and Douglass, 1986). In flume challenges, Frenzl (2014) found maximum sensitivity of copepodids to light at 455 nm. In addition to the response to constant light, evidence for a response to changing light intensities/shadows (scototaxis) in adult sea lice (authors' qualitative observations) and copepodids (Fields *et al.*, 2017) strongly indicates a behavioural response toward moving objects obstructing or reflecting light.

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 recognized photopositive behaviour of copepodid stages, a number of authors observed successful settlement or attempted settlement in darkness (Johnson and Albright, 1991b; Bron *et al.*, 1993; Heuch *et al.*, 2007; Frenzl, 2014), although settlement success was generally lower than when under illumination. 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 (Heuch *et al.*, 1995). 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 (Bron *et al.*, 1993; Heuch and Karlsen, 1997; Heuch *et al.*, 2007). Bron *et al.* (1993) and Gravil (1996) also demonstrated that copepodids are negatively geotactic, i.e. they swim toward the surface, 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 and 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 and Amundrud, 2007; Amundrud and 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.

Salinity

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 min) (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 downward. Given a choice, they will remain in full strength seawater. Energy is expended for osmoregulation and to maintain their position in the water column, as sinking rates increase with decreasing salinity due to water density changes (Bricknell *et al.*, 2006). It is likely that copepodids avoid areas of low salinity as they require increased energy expenditure, which reduces survival time (Torres *et al.*, 2002). As low salinities reduce the activity levels of copepodids, their ability to respond to host cues is reduced (Bricknell *et al.*, 2006).

Currents

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 and Whoriskey, 2004; Costello *et al.*, 2004; McKibben and 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 (Costelloe *et al.*, 1998a), but high concentrations coincide with the seaward migration of salmon smolts and the freshwater migration of adult salmon (Costelloe *et al.*, 1998a; McKibben and 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 vertical positioning to compensate for lack of long distance swimming capabilities, using tidal currents to migrate toward river mouths, although no evidence has been found to support this. 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 toward a particular location. It has been suggested that at some times of the year, a high concentration of copepodids near river mouths could result from hatching of egg strings from lice on adult salmon, which 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 might simply be due to salmon migrating rapidly upstream when river flow is high (Costelloe *et al.*, 1998a, b)

Host location

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 is also apparent whereby activated copepodids swim toward 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 and Birkett, 2009). Experiments have shown that *L. salmonis* copepodids are attracted to odours from salmon and sea trout, and behavioural activation and positive upstream chemotaxis occur in the presence of salmon-derived compounds (Devine *et al.*, 2000; Genna, 2002; Ingvarsdottir *et al.*, 2002; Bailey *et al.*, 2006). While both light and chemoreception elicit behavioural responses in the infective copepodids, it has been shown that the effect of light on the swimming response is stronger than that of responses elicited by olfactory cues and that the two sources of sensory cues may act in combination to give stronger and more persistent responses (Fields *et al.*, 2017). Non-host odours activate copepodids, but positive chemotactic movements are not observed, indicating that *L. salmonis* can discriminate between salmonid hosts and other non-host fish from their odour (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 and Birkett, 2009). Although the activity of copepodids appears to be affected by temperature, with reduced activity at lower temperatures (Tucker *et al.*, 2000b), 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. 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).

Infectivity

While some previous models of sea louse dispersion include a mortality factor, they do not account for variations in infectivity, i.e. the ability of a louse encountering a fish to infect it. Infection can be considered in terms of a two-phase process comprising a reversible attachment phase following contact and an irreversible settled phase during which the copepodid becomes physiologically committed and can no longer re-enter a free-swimming state. In the salmon louse, the former phase comprises initial copepodid attachment using the antennae (Bron *et al.*, 1991) followed by manoeuvres to embed the anterior of the cephalothorax. At some point following initial attachment, the copepodid commences feeding and starts the process of metamorphosis and moulting to the chalimus I stage. Although the precise triggers and point of irreversible commitment remain to be identified, antimicrobial peptides (AMPs) have been shown to affect *C. rogercresseyi* frontal filament development *in vitro* (Núñez-Acuña *et al.*, 2016). It is, therefore, 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, light, temperature, season, a range of host factors, and copepodid age. A further difficulty encountered in the literature is the somewhat nebulous concept of "infection success." For some authors, copepodids attaching to the fish are counted directly. However, given the reversible nature of initial attachment and difficulty of capturing fish without dislodging attached copepodids, such counts may be prove less accurate,

although they provide an estimate of successful contact and attachment. As an alternative, many authors only count infection success following the moult to chalimus I, at which point larvae are hard to dislodge due to the permanent frontal filament attachment. This latter approach, however, incorporates a far greater potential for the superposition of host immunity/site selection effects upon the successful completion of the copepodid instar.

Age at infection

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 7 days, and Tucker *et al.* (2000a) report a significant reduction in the calorific value of *L. salmonis* larvae over 7 days with a sharp decline after 5 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 8 days at 10°C, 50% of copepodids were only active when stimulated; after 8 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 1 day old and 14 ± 8.71% at 7 days old. At 7 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 (2014) found in flume challenges that maximal infectivity was obtained at 4 days post-moult to copepodid, with the infectivity of the cohort declining by 6 days through mortalities and lower infective capabilities. Tucker *et al.* (2000a) found that infection success (measured as the proportion of larvae used for infection that were found on the fish at day 5 after infection) was approximately 75% at 11°C and approximately 20% at 6.5°C in 1-day-old and 3-day-old copepodids, with infection success declining significantly in 7-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 7 days old is known from experiments with *L. salmonis* (Pedersen, 2009), but detailed temporal infectivity profiles have not been published. 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 was not observed to 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 suggests that key determinants of variability of larval infection levels in Atlantic salmon act prior to host settlement, i.e. within the black box comprising egg production to host contact.

Impacts of environmental variables on infection

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 45% at 26‰ (~14% infection), 55% at 19‰ (~10% infection), and 87.5% at 12‰ (~1% infection) compared to full-strength seawater, which was not wholly attributable to reduced survival at these salinities. At 4‰ no copepodids were found on the fish.

While settlement success is lower with reduced energy reserves, Samsing *et al.* (2016) used degree days to normalize copepodid energy reserves cultured at different temperatures; at 30 degree days from hatching, settlement success was 41.6 ± 2.0% at 20°C, 53.2 ± 2.3% at 10°C, and 2.1 ± 0.4% at 5°C. Key values for infectivity are shown in Table 5.

Post-attachment variables

A number of variables intervene between initial attachment of the copepodid and successful moulting to the chalimus I stage. In particular, once attached, the copepodid becomes susceptible to host defences, particularly in terms of innate host immunity, often expressed through inflammatory processes. The success of the host response in controlling infection depends upon a number of variables including the species/genotype of the host fish, its age, maturity, health and welfare/stress status, and interactions of immune capabilities with environmental parameters such as temperature. The role of the host in mediating infection success will only be covered briefly here as it has been extensively reviewed and investigated by previous authors (Skugor *et al.*, 2008; Tadiso *et al.*, 2011; Fast, 2014; Braden *et al.*, 2017 *inter alia*). In Atlantic salmon, initial infection by the copepodid can elicit a detectable transcriptomic host response within 1 day post infection (dpi) (Tadiso *et al.*, 2011) and some Pacific salmon species, e.g. juvenile coho, are able to mount a rapid and successful inflammatory response following infection (Johnson and Albright, 1992; Fast *et al.*, 2002; Jones, 2011) that is capable of killing infecting copepodids within a few days. Atlantic salmon show a less developed inflammatory response and are generally considered to show a poor capacity for removing infecting copepodids (Johnson and Albright, 1992). Despite this observation, different genetic stocks or families of Atlantic salmon can show significant differences in their capacity to resist infection, although the mechanisms

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

	Infectivity capability	Lipid reserves	Proportion
Copepodid age			
7–10d	Increasing[abcd]	Good[abcd]	–
11–15d	Mature[abcd]	Decreasing[abcd]	–
16–20d	Less capable[abcd]	Low[abcd]	–
Infection success at 10°C and 35 ppt			
1-day-old copepodids	–	–	22.22 ± 8.32%[c]
7-day-old copepodids	–	–	14 ± 8.71%[c]
Infection success aged 1–3d			
Illumination	–	–	23.2%[b]
No illumination	–	–	18.4%[b]
Infection success at 35 ppt			
5°C	–	–	2.1 ± 0.4%[e]
6.5°C	–	–	20%[d]
10°C	–	–	53.2 ± 2.3%[e]
11°C	–	–	75%[d]
20°C	–	–	41.6 ± 2.0%[e]
Infection success at 12°C			
12 ppt	–	–	1%[f]
19 ppt	–	–	10%[f]
26 ppt	–	–	14%[f]
34 ppt	–	–	31%[f]

References: (a) Cook *et al.* (2010), (b) Bron (1993), (c) Gravil (1996), (d) Tucker *et al.* (2002), (e) Samsing *et al.* (2016), (f) Bricknell *et al.* (2006). No infectivity data is available for *L. salmonis oncorhynchi*.

underlying differential resistance are currently poorly understood. Jodaa Holm *et al.* (2015) have suggested that differential resistance may reflect the ability of the host to avoid immunosuppression by the parasite. In a comparison of salmon family susceptibility, Gharbi *et al.* (2015) demonstrated a ∼60% difference in the median infection count at 7 dpi (chalimus I) for the least and most susceptible salmon families tested by copepodid infection challenge and calculated a genetic heritability of 0.3 for this trait making it a good candidate for selective breeding. The capacity of salmon to reduce infection success may also be modified by extrinsic factors such as diet and temperature. Functional feeds containing a range of active plant or bacterial extracts have, for example, been shown to have significant effects on infection success, providing infection reductions of up to 50% (Jensen *et al.*, 2014; Jodaa Holm *et al.*, 2016; Sutherland *et al.*, 2017).

Sea lice, like other arthropod parasites, can also suppress or redirect host immune responses by the use of a range of secretory excretory products (SEPs) including prostaglandin E-2, trypsin, peroxinectin and a range of other proteases, peroxidases, and potential defensin classes (Fast, 2014; Øvergård *et al.*, 2016). The success of the parasite in immunomodulating the host depends on the individual host's innate susceptibility and its state at the time of infection. Similarly, the status of the parasite can be important such that, for example, genetic family differences may affect infection success (Ljungfeldt *et al.*, 2014) although the point at which success is mediated and the mechanisms involved remain unknown.

Mortality through predation

Once sea lice have attached to a host, their chances of survival are increased 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 plankton and sessile filter feeders such as bivalve molluscs. Global approximations of the partitioning of wider zooplankton mortality suggest that predation accounts for 67–75% of total mortality in the plankton (Hirst and 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 plankton assemblages vary considerably according to season and location (e.g. Daewel *et al.*, 2014), and prey selection sizes vary amongst the different actively or passively predating species represented in the zooplankton community at any time (Hansen *et al.*, 1994; Wirtz, 2011, 2012). As a consequence of a lack of specific data, the following discussion seeks to provide guidance based on wider knowledge of zooplankton, which may be used by researchers to formulate research questions or provide initial parameters for models.

Plankton community structure

In regional marine ecosystems, several processes govern the structure and dynamics of plankton communities. These processes vary according to geographical location, resulting in distinct ocean regions with their own typical plankton assemblages. 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 (Kaiser, 2005).

These broad ocean regions may further be characterized according to ocean processes in different sub-regions, e.g. the North Sea, the Norwegian Sea. The abundance of different species that are

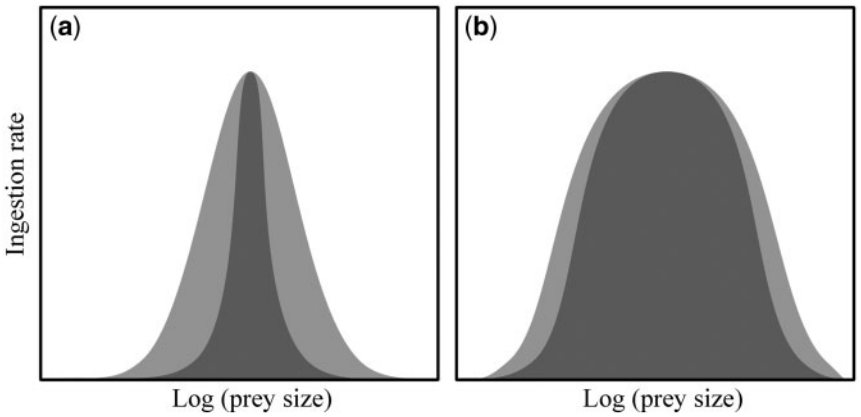

Figure 2. Typical ingestion (light grey area) and selection (dark grey area) feeding kernels for (a) narrow-range, selective feeders, e.g. copepods, and (b) broad-range, unselective feeders, e.g. jellyfish, where prey are abundant. Adapted and redrawn from Wirtz (2014).

predators of sea lice larvae and the abundance of other prey will affect the mortality rate of sea lice larvae. Therefore, providing data on larval predation by different plankton assemblages and characterizing the plankton assemblage at a specific location represents an important step in predicting mortality rates due to predation.

Predator selectivity

The body sizes of predator and prey are fundamental in the study of aquatic food webs (Brooks and Dodson, 1965; Woodward *et al.*, 2005). A "feeding kernel" represents a description of the probability of prey ingestion given as a function of feeding rate vs. prey size (Figure 2) (Visser and Fiksen, 2013; Wirtz, 2014). Selective grazing in the presence of a broad spectrum of prey size plays an important role in variable feeding relationships (Sommer and Stibor, 2002), and in the case of larval sea louse 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. Frost, 1972; Kiørboe and Saiz, 1995; Saiz and Kiørboe, 1995; Boenigk and Arndt, 2002; Visser *et al.*, 2009). This behavioural plasticity shrinks the overall spectrum of potential prey toward 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 (Figure 2). 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).

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 (1991a) 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 oncorhynchi* collected from British Columbian waters. Schram (1993) reports similar ranges for *L. salmonis salmonis* 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 (Kaiser, 2005).

Chaetognaths, or arrow worms, are important predators of copepods and are probably major contributors to the structuring of many marine ecosystems (Steele and Frost, 1977). 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 of a suitable size category.

Ctenophores, or comb jellies, are found throughout the world's oceans, and all are predatory, feeding on zooplankton (Fowler, 1911). If food is plentiful, they can eat ten times their own weight per day (Reeve *et al.*, 1978). 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}, hence similar in size to sea lice larvae, were most susceptible to predation by *P. bachei*, and later juvenile stages, which are larger, were less susceptible to predation (Greene *et al.*, 1986).

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 salmonid aquaculture (Doyle *et al.*, 2007). 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 and Sullivan, 1998). However, research has shown that scyphozoa are highly selective, and prey size has a significant impact on feeding rates (Suchman and 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 and Sullivan, 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 (Båmstedt and Karlson, 1998). While most are omnivorous filter feeders and feed on phytoplankton and detritus, some are carnivorous and feed on other zooplankton (Cripps and Atkinson, 2000). In the Norwegian Sea, the copepod *Calanus finmarchicus* (which has similar-sized juvenile stages to sea lice) is a dominant prey of euphausiid shrimp (Båmstedt and Karlson, 1998).

The larval stages of many 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 and 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. Some adult fish, such as scombrids and clupeids, feed on plankton throughout their lives, and switch between feeding modes depending on prey density (Janssen, 1976). 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 *et al.*, 1994).

In addition to planktonic predators, sessile feeders, particularly bivalve molluscs and cnidarians, could also have a 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 (Davenport *et al.*, 2000). 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 lice infections.

The foregoing observations on levels of predation of zooplankton support the suggestion that the mortality of free-living sea lice stages, i.e. nauplii and copepodids, is likely to be high during the planktonic phase.

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. 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 summarizes the factors reviewed in this study that may affect subsequent levels of infection.

A simplified conceptual framework can be employed to summarize 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:

$$S = EP_hP_pP_dP_sP_eI$$

Where S is number of successfully infecting copepodids, E is the number of eggs produced, P_h is the probability of hatching, P_p is the probability of avoiding predation, P_d is the probability of successful development from nauplii to copepodids, P_s is the probability of copepodid mortality due to senescence, P_e is the probability of encountering an appropriate host, and I is the mean infectivity of the copepodid population. The operational use of this conceptualized framework requires the estimation of the components of each of these variables, which are themselves influenced by a range of biotic (e.g. host) and abiotic (e.g. water temperature) factors and each other, i.e. they are not independent. As each component (or loss) is multiplicative, the uncertainties in each component may result in very wide error margins in S. Therefore, it is important to define and continue to refine each component through extensive data collection and parameterization to reduce the level of error.

By forming a table of these variables and the observable factors that may influence them (Table 6), 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 6). Furthermore, a lack of standardization and consistency across different studies due to various experimental conditions and the origin of experimental lice, e.g. of Atlantic or Pacific origin, 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 6), 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.

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 parameterization by experimental means. These are addressed below with reference to the conceptual framework defined above.

Egg production (E)*, egg viability, and hatching success* (P_h)

Previous estimates of egg production in the literature vary across more than an order of magnitude, are relatively inconsistent and

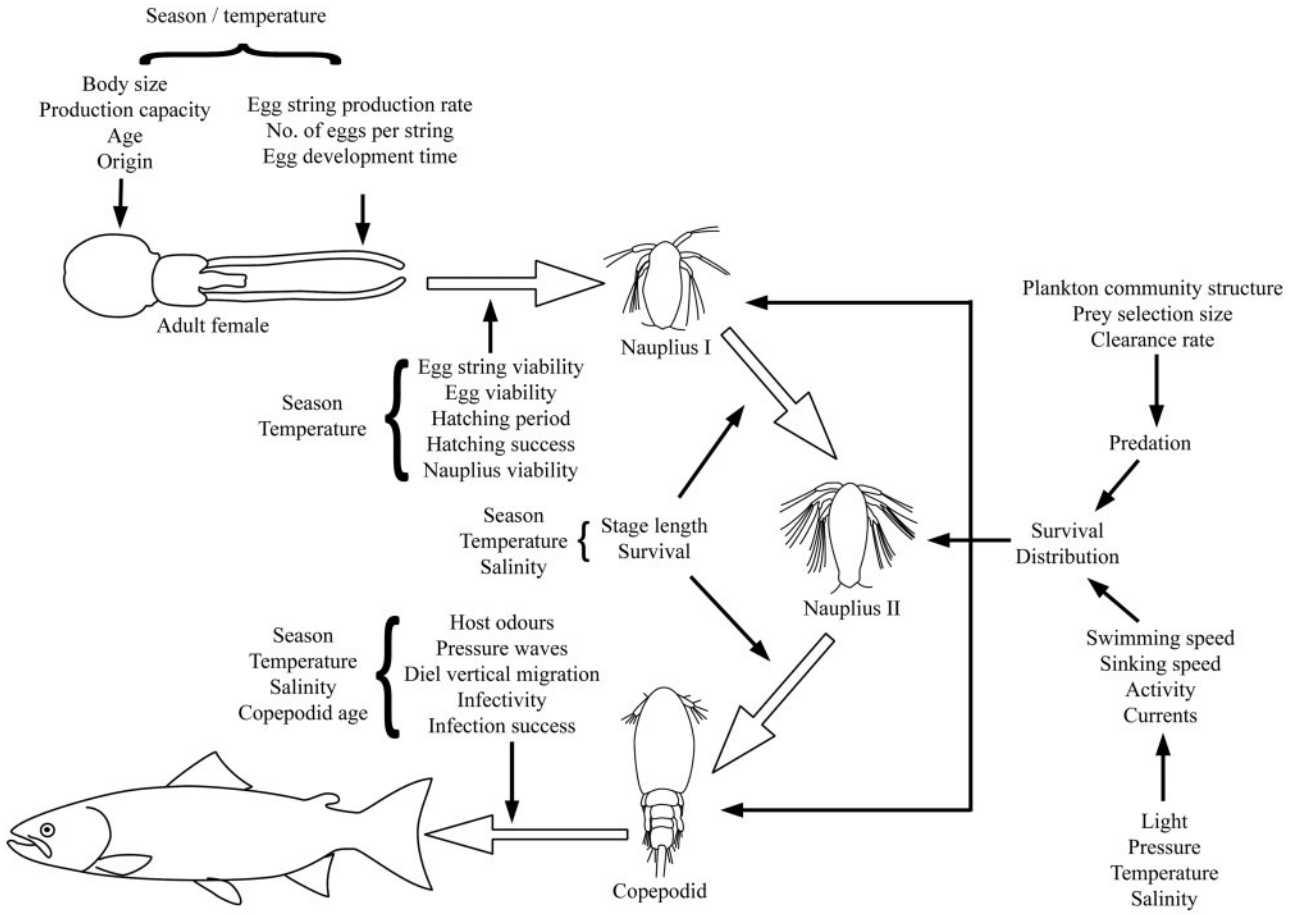

Figure 3. A conceptual model of the stages of the sea louse life cycle that determine the number of copepodids available for infection and their infection success with factors that may affect survival/infectivity at each stage. Open arrows show the life cycle and black arrows show the factors that may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

Table 6. 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.

	Variable factor					
Parameter	**Origin: wild/farmed**	**Temp.**	**Salinity**	**Light/photoperiod**	**Season**	**Reference**
Female size	X	X		X		a, b, c
Egg string production rate		X				a
No. of eggs	X	X		X		a, c, d, e, f, g
Egg development time		X				h, i, j
Egg development time		X				g
Hatching period		X	X			c, h
Egg viability		X	X	X		a, c, h
Hatching success		X	X	X		c, g, h
Nauplius I development time		X				c, g, h, i, j, k
Nauplius II development time		X				g, h, i, j, k
Nauplius I width					X	c
Nauplius I lipid reserve width					X	c
Survival to copepodid		X	X			c, i
Copepodid survival time		X	X			c, h, i

Cells marked with an X represent areas where some data already exist and blank cells represent areas of data deficiency. References: (a) Heuch *et al.* (2000), (b) Tully and Whelan (1993), (c) Gravil (1996), (d) Ritchie *et al.* (1993), (e) Johnson and Albright (1991a), (f) Tully (1992), (g) Samsing *et al.* (2016), (h) Johnson and Albright (1991b), (i) Johannessen (1977), (j) Boxaspen and Næss (2000), (k) Wootten et al. (1982).

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).

Egg production level is influenced by a broad range of factors including temperature (and temperature adaptation), salinity, host state (nutrition, immunity, stress, species, 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-recognized that egg strings sourced from lice on wild fish tend to have higher numbers of eggs (Tully and Whelan, 1993; Pike and Wadsworth, 1999).

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.

Predation in plankton (P_p)

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 coordinated 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 are 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.

Infectivity profile (I)

To date, there has been a tendency to equate the number of copepodids in the water column with the number of infecting individuals. From previous observations, however, it is apparent that there is a profile of infectivity, i.e. 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 toward death. Infection success requires definition as not all copepodids that attach to a host may establish a successful infection; the number of copepodids developing to the chalimus I stage and developing a permanent attachment via a frontal filament may be an appropriate measure of infection success. 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 challenging experiments employ static tanks and long exposure times, providing a totally inaccurate reflection of probabilities for real-world infection success.

While the infectivity profile needs to be better 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 is possible to profile the infectivity of copepodids with age and under different temperature and salinity conditions. However, a more accurate reflection of infectivity can 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 incurred between egg hatching and the reinfection of hosts is the detailed farm louse counts already conducted in many countries. Assuming knowledge of seasonal levels of egg production and viability, which may be easily obtained, the annual profile of copepodid/chalimus counts, can, at least for some more hydrographically constrained regions, provide an indication of the proportion of hatched larvae that successfully re-establish infections on fish.

Coordinated research

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

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, survival of free-swimming stages, and infectivity of survivors are key determinants of the number of lice re-establishing host 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 to manage timing of treatments appropriately, e.g. reflecting larval predation following spring algal blooms. While many aspects of louse biology are important in determining the number of lice available for infection, care should be taken to avoid the over-parameterization 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 IPM 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 minimize the environmental and economic impact of these pathogens on farmed and wild salmonids.

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