

1 This is a pre-copyedited, author-produced version of an article accepted for
2 publication in *ICES Journal of Marine Science* following peer review. The version of
3 record A J Brooker, R Skern-Mauritzen, J E Bron, Handling editor: David Fields;
4 Production, mortality, and infectivity of planktonic larval sea lice, *Lepeophtheirus*
5 *salmonis* (Krøyer, 1837): current knowledge and implications for epidemiological
6 modelling, *ICES Journal of Marine Science*, Volume 75, Issue 4, 1 July 2018, Pages
7 1214–1234 is available online at: <https://doi.org/10.1093/icesjms/fsy015>.

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

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26 **Abstract**

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

42

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

44

45 ***1 Introduction***

46 The parasitic copepods known as sea lice remain a key constraint to the continued growth of
47 salmonid aquaculture industries worldwide. In the North Atlantic, *Lepeophtheirus salmonis*
48 *salmonis* (Krøyer, 1837) is the primary species infecting cultured Atlantic salmon (*Salmo*
49 *salar* L.), whereas in the North Pacific, *Lepeophtheirus salmonis oncorhynchii* (Johnson and
50 Albright, 1991a) is prevalent in cultured salmon, although *Caligus elongatus* von Nordmann,
51 1832 also has some impact. In the southern hemisphere *Caligus rogercresseyi* Boxshall and
52 Bravo 2000 is the principal pathogenic species affecting the Chilean salmon aquaculture
53 industry. For the Norwegian salmon industry, where costs are best characterised, the economic
54 impact of sea lice was estimated to be in excess of 3.4 billion NOK per annum (>£300M) in
55 2014 for 1,272,358 tonnes production (Iversen *et al.* 2015) with costs estimated to exceed 5
56 billion NOK (>£390M) in 2015 for 1,303,346 tonnes = 3836.28 NOK tonne⁻¹ (Iversen pers.
57 comm.). Higher estimates of 7–8 billion NOK per annum (>£540M) have also been presented
58 (Rødseth, 2016). Using FAO statistics for global cultured Atlantic salmon production in 2015
59 (<http://www.fao.org/fishery/statistics/global-aquaculture-production/en>) for all countries that
60 experience sea lice problems (2,332,290 tonnes) and Iversen's estimate of cost per tonne for
61 2015 ($3836.28 \times 2,332,290$) provides a rough cost estimate of ~9 billion NOK globally for
62 2015 (~£700M), with costs likely to have continued to rise since then.

63 Current integrated pest management (IPM) strategies for sea lice control rely on a small
64 number of licensed pesticides, few of which are effective against all stages of the parasite's
65 life cycle, combined with effective husbandry management tools, such as single-cohort
66 stocking, optimised stocking densities, the use of cleaner fish in polyculture and fallow periods
67 (Skiftesvik *et al.* 2013; Leclercq, *et al.* 2013). Physical techniques to exclude lice, such as the
68 use of barrier nets and snorkel cages, coupled with mechanical tools, including thermal and

69 turbulent de-licers and laser removal, also constitute an increasing component of current IPM
70 strategies. The adoption of such an increasingly multimodal approach means that the timing
71 of management decisions is critical to the successful control of the parasite. A central element
72 required for the prediction of fluxes in lice populations is an understanding of the production,
73 survival, dispersal, development and infectivity profile of the free-swimming non-infective
74 nauplii and infective copepodid larval stages. However, despite more than three decades of
75 research, knowledge in this area remains extremely poor.

76 Within the past ten years, several models have been developed that attempt to estimate lice
77 burdens on wild and cultured salmon by predicting the production and distribution of lice
78 larvae from salmon farms and the subsequent risk of transmission. Although complex physical
79 coastal processes can now be reasonably accurately modelled, aspects of larval behaviour and
80 mortality often appear oversimplified. This knowledge gap has serious consequences as it
81 confounds the realistic estimation of the number of lice capable of infecting wild and cultured
82 salmonid populations.

83 In ecological terms, sea lice can be considered r-strategists, which are characterised by small
84 body sizes, high fecundities and short generation times. Although offspring of r-strategists are
85 dispersed widely, they have a low probability of survival (Cavaleiro & Santos, 2014).
86 However, sea lice differ from many other r-strategists in that they are attached to a host, which
87 provides a permanent food source and allows anomalies, such as a larger body size, and raises
88 the question of whether they have a high fecundity because they experience heavy losses
89 during the larval stages or because they have a nominally unlimited food source. The high
90 fecundity and wide larval dispersal are key aspects of the sea louse's life cycle that determine
91 its overall survival and success. As a result, fecundity and larval biology should be the focus
92 of efforts to predict lice burdens on fish. In the life cycle of the sea louse, however, the free-

93 swimming stages are essentially a ‘black box’ that cannot be easily observed directly from
94 field studies. Once a copepodid has attached to a host, development is more predictable as
95 development after infection is unaffected by copepodid age at infection (Tucker *et al.* 2000a;
96 Pedersen, 2009), although at this point host factors such as host species / genotype, immunity
97 and site of infection intervene to affect success. Transmission is still a contentious issue with
98 disagreement over whether lice (despite water currents) are accumulated at their source (*e.g.*
99 Krkošek *et al.* 2005 and implied by Jansen *et al.* 2012) or hydrodynamically spread over large
100 distances (*e.g.* Brooks, 2005; Asplin *et al.*, 2014). Therefore, accurate data are urgently needed
101 to inform and validate increasingly realistic models of larval dispersion and infectivity that
102 combine physical processes with key aspects of lice biology to successfully predict larval
103 dispersion and infection risk.

104 Early models for predicting lice burdens rely on the relationship between gravid female lice
105 and infective larval stages, based on factors such as fecundity, mortality and moult timings, to
106 predict future cohorts of lice available to infect fish (*e.g.* Heuch & Mo, 2001; Murray, 2002;
107 Tucker *et al.* 2002). Although these models can predict louse numbers within a simple closed
108 system, they cannot be applied to large, open systems, such as fjordic sea lochs where salmon
109 are commonly farmed, as they do not take into account larval dispersion and exogenous
110 sources of mortality, such as predation.

111 Particle tracking models predict the dispersal over time of particles generated at a point source
112 using hydrodynamic models (*e.g.* Corner *et al.*, 2006), which calculate local current velocities
113 based on local topography, fluid dynamics and external forcing from tidal elevation,
114 freshwater inputs and wind-generated currents. Early attempts to predict the dispersal of sea
115 lice larvae using a particle tracking model were made by Asplin *et al.* 2004 who estimated the
116 dispersal of lice from a salmon farm in Sognefjord, Norway. Detailed currents, hydrography

117 and wind forcing are calculated using high-resolution, three-dimensional ocean and
118 atmospheric models, and although a temperature-dependant larval growth model is included,
119 there is no estimation of larval mortality or behaviour. It assumes that lice are immortal with
120 passive behaviour, and consequently, the dispersal of lice is overestimated with larvae being
121 spread over a distance of 100km in just a few days (Asplin *et al.* 2004).

122 In order to accurately estimate infection risk, it is clear that certain aspects of louse biology,
123 such as survival, mortality and development times, need to be incorporated into these types of
124 models, and more recent models have attempted to do this. Murray and Amundrud (2007) and
125 Amundrud and Murray (2009) present a coupled biophysical and particle tracking model of
126 Loch Torridon, Scotland that incorporates development times as a function of temperature and
127 a fixed mortality rate based on laboratory observations.

128 More recent models have become increasingly complex, and Asplin *et al.* (2011 and 2014)
129 present a model of a Norwegian fjord comprising a number of sub-models: a coastal ocean
130 model, an atmospheric model, a fjord model, and a salmon louse growth and advection model.
131 While the salmon louse sub-model includes relevant parameters regarding stage timings, it
132 only includes a few simple behavioural parameters, *i.e.* a diel vertical migration, limited to
133 depths above 10 m and avoidance of salinities below 20 ‰; however, it does not calculate
134 louse mortality. A further model by Stucchi *et al.* (2011), which models the hydrographically
135 complex Broughton Archipelago in British Columbia, Canada, includes a comprehensive sub-
136 model of egg production, larval development, mortality and behaviour using data from the
137 literature, including the effects of temperature and salinity on these parameters. In addition, a
138 recent model similar to the one utilised by Asplin *et al.* (2014), which uses a mortality rate of
139 17 %, predicts that larval behaviour potentially has significant effects on advection (Johnsen
140 *et al.* 2014).

141 Aldrin *et al.* (2013) and Kristoffersen *et al.* (2014) present a model based on a statistical
142 network of Norwegian salmon farms. Monthly external and internal infection pressure and the
143 risk of infection between neighbouring farms are predicted based on lice burden estimates
144 from the previous month and the distances between neighbouring farms. The model is fitted
145 to actual lice counts from Norwegian farms between 2003 and 2011. It uses temperature-
146 dependent fecundity and larval demographics, although mortality rates for free-swimming
147 larvae and chalimus stages are fixed.

148 While these models have made significant progress in predicting larval dispersal in semi-
149 enclosed water bodies, model validation with field data is difficult, and there are always
150 discrepancies between the model output and field observations. For example, Salama *et al.*
151 (2011) and Adams *et al.* (2012) found very few larval sea lice in plankton tows in areas where
152 models had predicted high numbers. However, correlation between predicted and observed
153 infections appear to be more accurate for the model developed by Sandvik and colleagues
154 (Sandvik *et al.*, 2014). Model variables are based on the best available data, and while accurate
155 topography and hydrography data can easily be obtained, detailed information regarding the
156 life history of sea lice is often lacking, despite over three decades of research in this area.
157 Where models incorporate larval mortality, for instance, they use a constant mortality at each
158 larval stage, which may be kept constant (*e.g.* Aldrin *et al.*, 2013; Johnsen *et al.*, 2014) or vary
159 according to salinity (*e.g.* Amundrud and Murray, 2009; Adams, 2012). In reality, however,
160 larval mortality is extremely variable according to temperature, salinity, season, moult stage
161 and predation in the plankton, *etc.* While some data are available regarding these different
162 parameters, others are distinctly lacking, and more research is required in these areas.
163 Acquiring experimental data on these variables will allow the more realistic parameterisation
164 of key elements relating to abundance and infectivity of free-swimming larval sea louse stages

165 for incorporation into models that may more accurately predict the risk of infection under
166 various environmental conditions.

167 Some models are now considered sufficiently developed to warrant their use as components
168 of an integrated sea louse management strategy. For example, Norwegian salmon farming will
169 from 2017 be regulated regionally through an operational management system comprising the
170 application of predictive models that predict louse infection intensities along the entire
171 coastline (Asplin, 2014), combined with a process of continuous model validation and
172 calibration against real-world data (Bjørn *et al.* 2014, Sandvik *et al.*, 2016).

173

174 The aims of this review and analysis were as follows:

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

182

183 Additional considerations:

- 184 • While this review focuses primarily on *Lepeophtheirus salmonis spp.*, observations
185 from other species that are problematic in salmonid aquaculture are also noted where
186 appropriate.
- 187 • This review also focuses principally on knowledge concerning louse larvae deriving
188 from farmed fish due to both their greater accessibility and the fact that environmental

189 parameters can only be sufficiently controlled or consistently measured in defined
190 water masses.

191 • Hitherto, there has been some conflation of data arising from Atlantic and Pacific sea
192 louse studies. Evidence for clear genomic and phenotypic differences between these
193 subspecies has made it evident that the origin of data regarding these subspecies should
194 be considered when interpreting the results.

195 **2 Larval recruitment and survival**

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

202

203 **2.1 Fecundity**

204 The fecundity of sea lice varies considerably, and early observations showed that a single egg
205 string can contain <100–700 eggs (Wootten *et al.* 1982). Many studies have shown that
206 exogenous factors, such as temperature, photoperiod, salinity and food availability, interact
207 with endogenous factors to determine fecundity in crustaceans (*e.g.* Koop & Field, 1980;
208 Williams, 1985; Johnston & Dykeman, 1987, Maranhão & Marques, 2003). Similarly,
209 variations in the levels of sea lice infection between seasons and under different environmental
210 conditions suggest alterations in reproductive output in response to fluctuating environmental
211 parameters (Ritchie *et al.* 1993).

212 It is clear that temperature has a strong influence on fecundity (Tully, 1989), and the number
213 of eggs per string is positively correlated with female body size (Tully & Whelan, 1993).
214 Heuch *et al.* (2000) found that adult female lice of wild origin in Norway were significantly
215 larger than adult female lice of farm origin. Despite seasonal variations, lice of wild origin in
216 Ireland were similarly found to be significantly larger and carried approximately twice as
217 many eggs as lice of farm origin (Tully & Whelan, 1993). A similar pattern was reported by
218 Pike and Wadsworth (1999), who noted that female lice of wild origin produced 965 ± 30.1
219 eggs per egg string pair compared to 758 ± 39.4 and 297 ± 19.1 for lice originating from
220 untreated and treated farmed salmon, respectively, on the West Coast of Ireland. At 7.2 °C,
221 females were observed to produce a new pair of egg strings on average 11 days after the first
222 pair were removed, while at 12.2 °C this period was reduced to 5 days, and this continued for
223 the reproductive life of the female, with an average of 4.95 pairs of egg strings per female
224 under experimental conditions (Heuch *et al.* 2000). In this experiment, the first pair of egg
225 strings was always significantly shorter with the mean number of eggs increasing from 152
226 eggs per string to 285 eggs per string for subsequent egg strings, whereas Johnson and Albright
227 (1991b) recorded a mean number of eggs per string of 344.6 ± 79.8 in lice cultured at 10 °C
228 and 30 ‰ originating from wild and farmed chinook salmon (*Oncorhynchus tshawytscha*)
229 and farmed Atlantic salmon. Similarly, Gravid (1996) recorded a mean of 141.09 ± 22.19 eggs
230 per string for the first pair of egg strings, 216.4 ± 67.59 eggs per string for the second pair of
231 egg strings and 208.2 ± 50.97 eggs per string for the third pair of egg strings. It appears that
232 there may be a difference in the batch size in Atlantic *L. salmonis salmonis* (Heuch *et al.* 2000
233 and Gravid 1996) and the Pacific *L. salmonis oncorhynchi* (Johnson and Albright 1991a),
234 which highlights the importance of discriminating between the two subspecies (Skern-
235 Mauritzen *et al.*, 2014). Fecundity was found to be lower in *C. elongatus* with the number of

236 eggs per string being 52.62 ± 17.08 in *C. elongatus* compared to 206.2 ± 74.09 in *L. salmonis*
237 at 14 °C (Gravil, 1996). Key values for fecundity are shown in Table 1.

238 Ritchie *et al.* (1993) and Gravil (1996) investigated the reproductive output of *L. salmonis*
239 from salmon farms on the West Coast of Scotland and found that the number of eggs per string
240 was negatively correlated with temperature, with significantly more eggs being produced in
241 winter and early spring than in summer and autumn (Figure 1). In Ritchie *et al.* (1993), the
242 mean number of eggs per string increased significantly from 147 to 246 between October and
243 March (temperature range 12–5 °C) before decreasing to 175 eggs per string in August (13
244 °C). A similar pattern was seen by Gravil (1996), who found that the number of eggs per string
245 ranged from 194.1 ± 66.8 in October to 286.9 ± 64 in March. There appears to be a period of
246 lag of egg string length in response to temperature as the lowest temperature was recorded in
247 February whereas the longest egg strings were found in March, and this lag may reflect the
248 time required for egg strings to develop before being extruded at low temperatures. Samsing
249 *et al.* (2016) found a similar trend in lice acclimatised in the laboratory at different
250 temperatures with the number of eggs per string increasing from $\sim 135 \pm 5$ at 20 °C to $\sim 295 \pm$
251 10 at 5 °C. In the same experiment, it was found that the number of eggs per string produced
252 at 3 °C was lower ($\sim 153 \pm 10$) than at the higher temperatures tested. This decrease
253 corresponded to a decreased body size and coincided with a failure in larval development, and
254 it was speculated that this temperature could be close to the limit of their biological tolerance,
255 at least for the tested lice (Samsing *et al.*, 2016).

256 A variety of other factors may also affect lice fecundity. As an example, host condition and
257 the use of chemotherapeutants have been proposed as possible influences on egg string length
258 and the viability of larvae (Tully & Whelan, 1993). Likewise, fecundity may vary with host
259 species, either as a result of diet, the physiological status of the fish or genetic variation

260 (Johnson & Albright, 1992; MacKinnon *et al.* 1995; Mackinnon, 1998). This follows from the
261 intimate metabolic associations between hosts and parasites, which are often reflected in the
262 evolution of their genomes (e.g. Zarowiecki & Berrimann, 2015). It has also been suggested
263 that host immune responses may modify lice fecundity. For instance, Grayson *et al.* (1995)
264 found that gravid female lice on Atlantic salmon injected with extracts derived from adult *L.*
265 *salmonis* had a significantly lower fecundity than control fish. Similarly, Nilsen (2016) has
266 presented work suggesting that use of a recombinant vaccine to the salmon louse Ls4D8
267 protein, a homologue to subolesin in ticks and my32 in *C. rogercresseyi*, gave rise to reduction
268 in egg strings. Host-related and abiotic conditions may not be the only factors governing
269 salmon louse fecundity. As an example, intraspecific competition between lice on a given host
270 is suggested to result in reduced fecundity with increasing salmon louse infection densities
271 (Ugelvik *et al.*, 2017). Louse fecundity is clearly the product of a number of biotic and abiotic
272 factors, most of which remain to be fully characterised.

273

274 **2.2 Hatching**

275 Egg strings with non-viable eggs are sometimes extruded, and Heuch *et al.* (2000) found that
276 this happened most frequently in the second and third batches of egg strings. Gravid (1996)
277 reported that 2.1 % of egg strings consisted entirely of non-viable eggs. According to Heuch
278 *et al.* (2000), the number of viable eggs per string varied according to temperature, with a
279 median of 13.3 % of eggs being non-viable at 7.2 °C and 7.5 % being non-viable at 12.2 °C.
280 Similarly, Samsing *et al.* (2016) found that hatching success was strongly influenced by water
281 temperature, with 100 % success at 20 °C and 15 °C decreasing to 28 ± 4 % success at 3 °C.
282 Conversely, Gravid (1996) found no correlation between egg viability and temperature in *L.*
283 *salmonis* on farmed salmon on the West Coast of Scotland with a mean of 17.66 ± 23.01 %

284 non-viable eggs over one year. In comparison, the mean number of non-viable eggs per string
285 in *C. elongatus* was 28.19 ± 24.81 %, with 18.33 % of egg strings entirely consisting of non-
286 viable eggs (ibid.).

287 Salinity has a considerable effect on hatching, and egg strings maintained at 10 °C and 10 ‰
288 salinity failed to develop in Johnson and Albright's (1991b) experiments. At salinities of 15
289 ‰ and 20 ‰, hatching success was 70 % and 78 %, respectively, but only at 20 ‰ were any
290 active nauplii produced (19.8 %). At salinities of 25 ‰ and above, hatching success was 100
291 %, but at 25 ‰ only 51.1 % of nauplii were active, whereas at 30 ‰ this figure was 65.9 %.
292 Gravil (1996) reports a similar pattern with hatching success ranging from 3.27 % in
293 freshwater to 86.36 % at 30 ‰ salinity. The effect of photoperiod was investigated by Gravil
294 (1996), but it had no effect on hatching period or success. Key values for hatching are shown
295 in Table 2.

296 The hatching period is variable, and Johnson and Albright (1991b) report that it ranged from
297 18 to 65 h, with a mean of 31.7 ± 13 h for egg strings incubated at 10 °C and 30 ‰ salinity.
298 The authors of the current review consider these to be at the extreme end of hatching periods
299 observed based on personal observations, although this may represent a difference between
300 Atlantic and Pacific *L. salmonis*.

301

302 **2.3 Stage timings**

303 Development times are highly dependent on temperature and have been addressed in various
304 studies summarised in Table 3. Overall, the egg development time varies between 1.8–45.1
305 days for temperatures ranging between 2–20 °C (Johnson & Albright, 1991b, Boxaspen &
306 Næss, 2000, Samsing *et al.*, 2016). The duration of the first nauplius stage varies between 9.2–
307 52 h at temperatures ranging between 5–15 °C, while the corresponding duration for the

308 second nauplius stage varies between 33–170.3 h for temperatures ranging between 5–19 °C
309 (Johannessen, 1977, Wootten *et al.*, 1982, Johnson & Albright, 1991b, Gravid, 1996).
310 Durations of the stages seem to be comparable for Pacific and Atlantic lice, and reported
311 ranges agree with the ranges found in publications where developmental times were reported
312 for both naupliar stages combined (Gravid, 1996, Boxaspen & Næss, 2000, Samsing *et al.*,
313 2016). While temperature has a considerable effect on egg production and larval development,
314 photoperiod does not appear to have any significant effect (Ritchie *et al.* 1993; Gravid, 1996).
315 The time required for physically moulting (exuviation) from nauplius I to nauplius II and
316 nauplius II to copepodid are reported as 10.53 ± 4.34 mins and 12.21 ± 3.87 mins, respectively,
317 and during the moult the larvae are inactive and sink through the water column (Gravid, 1996).
318 It appears that the temperature of acclimation of adult female lice is important in determining
319 the temperature tolerance of their eggs and larvae. Johannessen (1975) reports that in adult
320 lice cultured at 9 °C, nauplius development occurred only between 8–11 °C, whereas
321 acclimation at 11.5 °C allowed larval development up to 22 °C. In adult lice maintained at 3
322 °C, however, nauplii failed to develop to copepodids (Samsing *et al.*, 2016).

323

324 **2.4 Survival**

325 Nauplii that hatch successfully are planktonic. At this stage they do not feed, but are
326 lecithotrophic (yolk feeding) and rely on their energy reserves until they moult to infective
327 copepodids and find a suitable host (Johnson & Albright, 1991b). The survival of sea lice and
328 the rate at which they deplete their energy reserves are strongly influenced by temperature and
329 salinity. The size of larvae and their lipid stores is also dependant on season, and Gravid (1996)
330 reports that nauplius I larvae were largest in August with a mean body width of 214.05 µm
331 and a mean lipid reserve width of 135.84 µm compared to 197.76 µm and 112.98 µm in May

332 for mean body width and mean lipid reserve width, respectively. It is likely that increased
333 energy reserves will increase the longevity or compensate for a higher temperature-dependent
334 metabolism of the non-feeding larval stages, although no data are available comparing survival
335 at different times of year.

336 Johnson & Albright (1991b) report that active copepodids were only obtained at salinities
337 above 30 ‰ at 10 °C (35.2 % active), although survival was extremely variable ranging from
338 0–80.6 % per egg string. Similarly, Gravid (1996) found that copepodids were only obtained
339 at salinities greater than 25 ‰, and at 10 °C and 35 ‰, 18.33 % reached the infective
340 copepodid stage with nearly 50 % mortality being seen in the nauplius I stage. Samsing *et al.*
341 (2016) found that sea lice larvae from Scotland did not proceed past the nauplius II stage at 5
342 °C and 3 °C, respectively, but died before moulting to copepodids, and at 7.5 °C, very few
343 copepodids were obtained (Gravid, 1996). In sea lice adapted to low temperatures, however,
344 copepodids were obtained from 25 % of egg strings reared at 2 °C, 42 % at 3 °C, 100 % at 4
345 °C and 75 % at 5 °C (Boxaspen and Næss, 2000). In *C. elongatus*, Pike *et al.* (1993) report 90
346 % survival from the nauplius stage to the copepodid stage at 15 °C with this figure decreasing
347 to 60 % at 5 °C.

348 As with all copepods, sea lice have preferred environmental conditions, which are determined
349 by their physiological tolerances. Copepodids that were transferred from full-strength
350 seawater to 5 ‰ salinity survived for just 3 h at 10 °C, and those transferred to 10 ‰ salinity
351 survived for less than one day (Johnson & Albright, 1991b). A similar experiment by Gravid
352 (1996) found that the median survival time was 14.87 h at 0–10 ‰. While copepodids can
353 osmoregulate above 16 ‰, their haemolymph becomes rapidly diluted below 12 ‰, and they
354 are unable to regulate cell volume and die within a few hours (Hahnenkamp & Fyhn, 1985;
355 Pike & Wadsworth, 1999).

356 Once nauplii moult to copepodids, they need to find a suitable host before their lipid reserves
357 are depleted, and the rate at which this occurs is also influenced by temperature and salinity.
358 Hyperosmotic regulation is energetically costly, and an increased energy demand significantly
359 reduces the survival time of copepodids due to their limited energy reserves (Torres *et al.*
360 2002). Johnson and Albright (1991b) report that survival was prolonged at salinities of 15–30
361 ‰ and temperatures of 5–15 °C, and that mean survival times were between two and eight
362 days. Similarly, Wootten *et al.* (1982) report that the mean survival time of copepodids at 12
363 °C was 4 days at an unspecified salinity. In Gravid (1996), the median survival time of
364 copepodids was 54 h at 15 ‰, 67 h at 20 ‰, 68 h at 25 ‰, 55 h at 30 ‰ and 64 h at 35 ‰,
365 which reflects the increased energy required for hyperosmotic regulation at lower salinities.
366 Conversely, Bricknell *et al.* (2006) report the median survival time of *L. salmonis* copepodids
367 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
368 h at 36 ‰. The reason for the differences in survival times reported in Gravid (1996) and
369 Bricknell *et al.* (2006) is unknown, although Bricknell *et al.* used copepodids that were a few
370 days old and cultured them with aeration whereas Gravid used unaerated containers.

371 According to Johnson and Albright (1991b), the maximum survival time was 17 days at 10 °C
372 and 25 ‰ salinity, and copepodids in lower salinities (15–20 ‰) were generally less active
373 than those maintained at higher salinities (25–30 ‰). In full strength seawater (35 ‰), the
374 maximum survival time of copepodids at 10 °C was 18 days (Gravid, 1996). Due to the reduced
375 hatching success and subsequent low survival of *L. salmonis* in low salinities, it is likely that
376 they may be excluded from salinities less than 15 ‰ (Johnson & Albright, 1991b), and survival
377 is severely compromised at salinities below 29 ‰ (Tucker *et al.* 2000b). Although survival is
378 reduced at lower salinities, short-term exposure to reduced salinities does not have a long-term
379 impact on the development of surviving copepodids (Bricknell *et al.* 2006). Attachment to a

380 host was not observed to improve survival at reduced salinities (Hahnenkamp & Fyhn, 1985)
381 and these authors suggest that, unlike adult lice, the copepodid and chalimus stages are unable
382 to use ions obtained from their host to replace those lost to a hypo-osmotic environment.
383 However, it appears likely that due to their small size, attached larvae will receive at least
384 some protection from reduced salinities through boundary layer effects coupled with close
385 contact with the host/host mucus, and it is also clear that as these are feeding stages, some
386 protection would be received from ingested host tissue.

387 The survival time of copepodids is inversely related to temperature, and Samsing *et al.* (2016)
388 report that the survival time of 80 % of copepodids was 12.5 days at 7 °C, 13 days at 10 °C,
389 9.5 days at 15 °C and 6 days at 20 °C; at 5 °C it was reduced to 10 days. This pattern is
390 presumably due to lower metabolism and, therefore, increased longevity of energy reserves at
391 lower temperatures, although at very low temperatures there appear to be other factors limiting
392 survival. Median survival times reported by Gravid (1996) were 116 h at 5 °C, 90 h at 10 °C
393 and 82 h at 15 °C at full salinity (35 ‰), although these appear to be gross underestimations
394 and may be due to sub-optimal culture conditions. There is, however, a seasonal investment
395 by adult females in reproduction as nauplii are larger and have larger energy stores in summer
396 than in winter (Gravid, 1996). At higher temperatures, metabolism is higher and larvae are
397 more active, so their energy stores are more rapidly depleted (*ibid.*). It is possible that the
398 increase in the size of larvae and their energy stores in summer may be a compensatory
399 mechanism to account for their energy stores being depleted more rapidly than in winter,
400 which ensures that their life expectancy is similar to that at colder winter temperatures. Further
401 experimental work is required to confirm this. Key values for survival are shown in Table 4.

402 **3 Behaviour**

403 While both of the free-swimming larval stages are planktonic, the nauplius stages of sea lice
404 are principally dispersal stages, whereas the copepodid stage must locate, re-establish contact
405 with and subsequently infect a suitable host. The larvae are subject to currents, which serve to
406 disperse them over a wide area, and although the larvae have limited movement capabilities,
407 their dispersal can be partially influenced by certain behaviours, *e.g.* aggregating at particular
408 depths in the water column (Johnsen *et al.*, 2014). In order to maximise their chances of
409 survival and host interception, they must be able to respond to cues present in their
410 environment and react to them appropriately. Their behavioural responses can be categorised
411 according to the following activities (Bron *et al.*, 1993):

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

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

420 ***3.1 Swimming speeds / activity***

421 Both nauplius and copepodid stages have been observed to actively swim upwards as they are
422 negatively buoyant, and their movements are punctuated by periods of passive sinking (Bron,
423 1993, Gravid, 1996). Haury and Weihs (1976) suggest that this behaviour theoretically saves
424 energy compared to continuous swimming at a fixed depth, which is particularly important for
425 the lecithotrophic larvae of *L. salmonis*, which must conserve their limited energy reserves
426 wherever possible. Despite their energy considerations, copepodids must maintain their

427 position in the water column where their chances of encountering hosts are highest (Bron,
428 1993). However, Gravid (1996) found the activity of nauplii and copepodids to be dependent
429 on temperature; at 5 °C their movements were reduced and they aggregated at the bottom of
430 containers, whereas at 10 °C and 15 °C they spent more time actively swimming than passively
431 sinking and aggregated at the surface. However, these results may be affected by insufficient
432 acclimation.

433 Copepodids swim more rapidly than nauplii and have longer swimming periods and shorter
434 rest periods (Bron, 1993). Gravid (1996) reports that the mean swimming speed of nauplii was
435 $1.25 \pm 0.16 \text{ cm s}^{-1}$, whereas the mean swimming speed of copepodids was $2.14 \pm 0.24 \text{ cm s}^{-1}$.
436 The mean sinking speeds were $0.09 \pm 0.01 \text{ cm s}^{-1}$ and $0.10 \pm 0.03 \text{ cm s}^{-1}$ for nauplii and
437 copepodids, respectively. In this study, the maximum speed recorded was 10.23 cm s^{-1} when
438 stimulated by vibration of the test chamber and gives an indication of the swimming ability of
439 copepodids. A similar one-second burst speed of 9 cm s^{-1} was recorded by Heuch and Karlsen
440 (1997), although speeds of 2 cm s^{-1} were sustained when stimulated. In comparison, reported
441 salmon swimming speeds are two orders of magnitude higher (Colavecchia *et al.* 1998). Thus,
442 while chemotaxis may be important in positioning the larvae in suitable water masses, the
443 pursuit of a salmon host, as opposed to the interception of it at close range, is not a viable
444 strategy.

445 Current speed and host swimming speed affect the ability of infecting copepodids to make
446 initial contact with the host and to remain attached following contact. Given the respective
447 speeds of copepodids and salmonids, the former cannot pursue the host but must intercept it
448 by burst-swimming when detecting it in the water column. The exposure time of the copepodid
449 to the host reduces with increasing current/host swimming speed, which in turn reduces the
450 window of opportunity for infection. In addition, the low-flow zone (boundary layer) caused

451 by drag at the surface of the fish, becomes thinner with increasing current/host speed, which
452 increases the exposure of the copepodid to the ambient water flow during attachment. This
453 means that at higher flows, the copepodid has less opportunity to make contact and is more
454 likely to be removed from the host by the current (Bron, 1993). The greater boundary layer
455 thickness and, hence, shelter from the ambient current offered by fin rays held perpendicular
456 to the direction of water flow is considered to provide some explanation of the observed greater
457 frequency of copepodid settlement on the fins of hosts (Bron, 1993, Bron *et al.*, 1993).
458 Similarly, the slower swimming speed of fish in tank challenges may explain the largely
459 artefactual attachment of copepodids to the gills in such trials, an observation rarely made
460 under field conditions (*ibid.*). While larger fish swim faster, this is offset by the provision of
461 a larger surface area for settlement and a greater boundary layer/shelter provided by larger
462 fins. Frenzl (2014) observed declining numbers of attaching copepodids with increasing
463 current speeds. Following a dose of 2,500 copepodids fish⁻¹ introduced in a flume challenge,
464 highest infection occurred at 0 cm s⁻¹ (mean 8.4 copepodids per fish) and lowest at 32.6 cm s⁻¹
465 (mean 0.2 copepodids per fish).

466 Little is known concerning the effects of competition for space and/or resources during
467 initial copepodid settlement. However, Frenzl (2014) has demonstrated a non-linear increase
468 of infection numbers with challenge dose in flume challenges, possibly suggesting the
469 increasing saturation of available settlement niches with increasing numbers available for
470 infection.

471 **3.2 Light**

472 Copepodids of *L. salmonis* are highly photopositive and move towards the illuminated zone
473 of the vessel in laboratory experiments even at low light intensities (Johannessen, 1975;
474 Wootten *et al.* 1982; Bron *et al.* 1993, Gravid, 1996). The nauplius stages are also

475 photopositive, but the nauplius I stage only exhibits a positive response at light intensities of
476 200 lux or more, whereas this value is 85 lux in the nauplius II (Gravil, 1996). Whereas nauplii
477 exhibit increasing activity with increasing light intensity, copepodids do not (ibid.). The free-
478 swimming larval stages of *C. elongatus* are also phototactic, with the copepodids showing a
479 contrasting greater response to light than the nauplii stages (Hogans & Trudeau, 1989). In *L.*
480 *salmonis*, a peak response was seen at a wavelength 500 nm in the nauplius II stage (Gravil,
481 1996) and 550 nm in the copepodid stage (Bron *et al.*, 1993, Gravil, 1996), and this
482 corresponds to the maximum transmitted light intensity at twilight, which may be a cue for
483 vertical migration in copepodids as suggested for free-living copepods (Forward & Douglass,
484 1986). In flume challenges, Frenzl (2014) found maximum sensitivity of copepodids to light
485 at 455 nm. In addition to the response to constant light, evidence for a response to changing
486 light intensities/shadows (scototaxis) in adult sea lice (authors' qualitative observations) and
487 copepodids (Fields *et al.* 2017) strongly indicates a behavioural response towards moving
488 objects obstructing or reflecting light.

489 Heuch *et al.* (1995) found a strong diel vertical migration in *L. salmonis* copepodids where
490 they gathered near the surface during the day and spread out into deeper layers at night. Despite
491 the recognised photopositive behaviour of copepodid stages, a number of authors observed
492 successful settlement or attempted settlement in darkness (Johnson & Albright, 1991b; Bron
493 *et al.*, 1993, Heuch *et al.*, 2007, Frenzl, 2014), although settlement success was generally lower
494 than when under illumination. As salmon remain in deeper waters during the day and rise to
495 the surface at night, they swim through a population of sinking or rising copepodids every 12
496 h (Heuch *et al.*, 1995). In addition, vertically migrating hosts produce stronger currents than
497 resting fish, and pressure waves in front of swimming fish trigger a looping behaviour allowing
498 nearby copepodids to avoid predation and attach to a host (Bron *et al.*, 1993; Heuch & Karlsen,

1997; Heuch *et al.*, 2007). Bron *et al.* (1993) and Gravid (1996) also demonstrated that copepodids are negatively geotactic, *i.e.* they swim towards 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 & 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.

3.3 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 minutes) (Gravid, 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. 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

523 reduces survival time (Torres *et al.*, 2002). As low salinities reduce the activity levels of
524 copepodids, their ability to respond to host cues is reduced (Bricknell *et al.*, 2006).

525 **3.4 Currents**

526 It has been proposed, although supporting evidence is lacking, that copepodids may actively
527 migrate to river mouths where high concentrations of salmon smolts are present at certain
528 times of year, which would increase their probability of encountering a host (Carr &
529 Whoriskey, 2004; Costelloe *et al.*, 2004; McKibben & Hay, 2004). Studies in estuarine areas
530 in Ireland suggest that copepodids are not found near the mouths of rivers for the majority of
531 the year (Costelloe *et al.*, 1998a), but high concentrations coincide with the seaward migration
532 of salmon smolts and the freshwater migration of adult salmon (Costelloe *et al.*, 1998a;
533 McKibben & Hay, 2004). As copepodids are capable of actively altering their position in the
534 water column, it is possible that they may be able to use vertical positioning to compensate for
535 lack of long distance swimming capabilities, using tidal currents to migrate towards river
536 mouths, although no evidence has been found to support this. As copepodids have been shown
537 to remain active in the water column (Bron *et al.*, 1993; Heuch *et al.*, 1995; Gravid, 1996),
538 they are distributed within a water body according to the prevailing currents and are, thus,
539 unlikely to directly influence their large-scale movement towards a particular location. It has
540 been suggested that at some times of year, a high concentration of copepodids near river
541 mouths could result from hatching of egg strings from lice on adult salmon, which often
542 congregate at river mouths prior to their migration upstream, particularly during periods of
543 low river flow (Jonsson *et al.*, 1990; Smith *et al.*, 1994). Similarly, the absence of copepodids
544 at river mouths during periods of high rainfall might simply be due to salmon migrating rapidly
545 upstream when river flow is high (Costelloe *et al.*, 1998a,b).

546 **3.5 Host location**

547 The responses of sea lice copepodids to physical cues, such as light and salinity, enable them
548 to gather in areas where host fish are likely to be found, and mechanical cues enable them to
549 infect a host. Chemoreception also plays an important role in host location, with copepodids
550 employing the cues provided by kairomones, specific chemicals released by host fish, to
551 improve the probability of host encounter. Copepodids swim with a general search pattern, but
552 once a host odour has been detected, a host-encounter search pattern is switched on, which
553 consists of increased duration and frequency of turning during the normal sinking and
554 swimming behaviour (Genna, 2002). A directional component is also apparent whereby
555 activated copepodids swim towards a suitable odour source over a distance of centimetres
556 (Bailey *et al.*, 2006), although a group of salmon might initiate a response over a scale of
557 metres (Mordue Luntz & Birkett, 2009). Experiments have shown that *L. salmonis* copepodids
558 are attracted to odours from salmon and sea trout, and behavioural activation and positive
559 upstream chemotaxis occur in the presence of salmon-derived compounds (Devine *et al.*,
560 2000; Genna, 2002; Ingvarsdottir *et al.*, 2002; Bailey *et al.*, 2006). While both light and
561 chemoreception elicit behavioural responses in the infective copepodids, it has been shown
562 that the effect of light on the swimming response is stronger than that of responses elicited by
563 olfactory cues and that the two sources of sensory cues may act in combination to give stronger
564 and more persistent responses (Fields *et al.* 2017). Non-host odours activate copepodids, but
565 positive chemotactic movements are not observed, indicating that *L. salmonis* can discriminate
566 between salmonid hosts and other non-host fish from their odour (Bailey *et al.*, 2006). In
567 comparison, *C. elongatus*, which is a generalist and infects many different species of fish,
568 demonstrates behavioural changes to chemical cues from a wide range of fish, although
569 physical cues may be more dominant in this species (Mordue Luntz & Birkett, 2009).
570 Although the activity of copepodids appears to be affected by temperature, with reduced
571 activity at lower temperatures (Tucker *et al.* 2000b), it is not known whether low temperatures

572 affect the switch to host-seeking behaviour and the distance over which they may be able to
573 detect host cues.

574 Despite their avoidance of areas of low salinity, the use of haloclines by copepodids has been
575 proposed as a host-finding mechanism, since host odours may accumulate in thin layers where
576 a density gradient occurs. In this respect, 80 % of copepodids were observed to aggregate at
577 the confluence of a 15–30 ‰ step-salinity gradient in laboratory experiments (Heuch, 1995).
578 In addition, positioning close to a halocline may increase the chance of encountering a host,
579 as salmon have been observed to follow salinity gradients (Lyse *et al.*, 1998; Finstad *et al.*,
580 2000)

581 **4 Infectivity**

582 While some previous models of sea louse dispersion include a mortality factor, they do not
583 account for variations in infectivity, *i.e.* the ability of a louse encountering a fish to infect it.
584 Infection can be considered in terms of a two-phase process comprising a reversible
585 attachment phase following contact and an irreversible settled phase during which the
586 copepodid becomes physiologically committed and can no longer re-enter a free-swimming
587 state. In the salmon louse, the former phase comprises initial copepodid attachment using the
588 antennae (Bron *et al.*, 1991) followed by manoeuvres to embed the anterior of the
589 cephalothorax. At some point following initial attachment, the copepodid commences feeding
590 and starts the process of metamorphosis and moulting to the chalimus I stage. Although the
591 precise triggers and point of irreversible commitment remain to be identified, antimicrobial
592 peptides (AMPs) have been shown to affect *C. rogercresseyi* frontal filament development *in*
593 *vitro* (Núñez-Acuña *et al.* 2016). It is, therefore, incorrect to assume that, once the copepodid
594 stage is reached, 100 % infection will occur (Gravil, 1996). Dispersion on currents and host
595 location behaviour bring the copepodids into the same locality as potential hosts, but the

596 process of infection is influenced by various factors, including salinity, light, temperature,
597 season, a range of host factors and copepodid age. A further difficulty encountered in the
598 literature is the somewhat nebulous concept of ‘infection success’. For some authors,
599 copepodids attaching to the fish are counted directly. However, given the reversible nature of
600 initial attachment and difficulty of capturing fish without dislodging attached copepodids, such
601 counts may be prove less accurate, although they provide an estimate of successful contact
602 and attachment. As an alternative, many authors only count infection success following the
603 moult to chalimus I, at which point larvae are hard to dislodge due to the permanent frontal
604 filament attachment. This latter approach, however, incorporates a far greater potential for the
605 superposition of host immunity / site selection effects upon the successful completion of the
606 copepodid instar.

607 ***4.1 Age at infection***

608 As lecithotrophic larval stages are reliant on their energy reserves for swimming, moulting
609 and host infection, the excessive depletion of these reserves prior to infection can result in the
610 loss of infective capability. As copepodids age, a higher proportion display reduced activity
611 due to the depletion of energy reserves or senescence (Bron, 1993). Gravid (1996) found that
612 the mean size of lipid vesicles in the mid-gut of copepodids was significantly reduced after
613 seven days, and Tucker *et al.* (2000a) reports a significant reduction in the calorific value of
614 *L. salmonis* larvae over seven days with a sharp decline after five days. By measuring stored
615 lipid volume, it is possible to determine age and viability in individual copepodids, and these
616 can be divided into three loose categories: early copepodids with an apparent increase in lipid
617 volume reflecting incorporation of naupliar lipids into distinct vesicles in the gut; mid-life
618 copepodids, which show a downward trend in lipid levels and may be the most active
619 individuals with mature infective capabilities; and late copepodids with low reserves of lipid,

620 which may be less capable of infection (Cook *et al.*, 2010). The depletion of energy reserves,
621 which consist primarily of lipids, might also result in a loss of buoyancy, making swimming
622 more energetically costly (Bron, 1993), although Gravid (1996) found no evidence to support
623 this. Gravid (1996) observed three stages of activity: newly moulted copepodids swam in
624 spontaneous bursts without stimulation; at eight days at 10 °C, 50 % of copepodids were only
625 active when stimulated; after eight days, remaining copepodids only showed activity after
626 being stimulated by a water jet from a pipette. This suggests that copepodids may adopt a
627 strategy of energy conservation if a host is not located after a certain period of time, and that
628 by only becoming active when stimulated, they preserve their remaining energy stores as long
629 as possible.

630 This reduced activity level affects infectivity, and Gravid (1996) reports that copepodid
631 infection success at 10 °C and 35 ‰ salinity was 22.22 ± 8.32 % at one day old and 14 ± 8.71
632 % at seven days old. At seven days old, approximately 20 % of copepodids were active without
633 stimulation and 40 % were active with or without stimulation. Bron (1993) reports similar
634 infection rates with 23.2 % settlement under illuminated conditions and 18.4 % settlement in
635 the dark for 1–3-day-old copepodids, although there was no significant difference in settlement
636 between light and dark conditions. For a cohort of copepodids hatched within 24 h, Frenzl
637 (2014) found in flume challenges that maximal infectivity was obtained at 4 days post-moult
638 to copepodid, with the infectivity of the cohort declining by 6 days through mortalities and
639 lower infective capabilities. Tucker *et al.* (2000a) found that infection success (measured as
640 the proportion of larvae used for infection that were found on the fish at day 5 after infection)
641 was approximately 75 % at 11 °C and approximately 20 % at 6.5 °C in one-day-old and three-
642 day-old copepodids, with infection success declining significantly in seven-day-old
643 copepodids, although lice in this experiment were collected and cultured at 10 °C before being

644 used in experiments, which may have affected the results. The ability of copepodids to infect
645 hosts past seven days old is known from experiments with *L. salmonis* (Pedersen 2009), but
646 detailed temporal infectivity profiles have not been published. However, infection success is
647 clearly linked to both the longevity and activity of the copepodid stage. Despite infection
648 success being dependent on copepodid age, the survival of copepodids once attached to a host
649 was not observed to differ between copepodids that infect at different ages (Tucker *et al.*,
650 2000a; Pedersen, 2009), which is likely due to the commencement of feeding once attached to
651 a host. This suggests that key determinants of variability of larval infection levels in Atlantic
652 salmon act prior to host settlement *i.e.* within the black box comprising egg production to host
653 contact.

654 ***4.2 Impacts of environmental variables on infection***

655 Host settlement success is also reduced at lower salinities, which coincides with a decrease in
656 their energy reserves (Tucker *et al.*, 2000a,b; Bricknell *et al.*, 2006). It is likely that the
657 physiological stress associated with reduced salinity rapidly depletes the energy reserves of
658 copepodids, which causes premature senescence and results in levels of settlement success
659 similar to those found in older copepodids (Bricknell *et al.*, 2006). These authors report that
660 infection levels were reduced by 45 % at 26 ‰ (~14 % infection), 55 % at 19 ‰ (~10 %
661 infection) and 87.5 % at 12 ‰ (~1 % infection) compared to full-strength seawater, which was
662 not wholly attributable to reduced survival at these salinities. At 4 ‰ no copepodids were
663 found on the fish.

664 While settlement success is lower with reduced energy reserves, Samsing *et al.* (2016) used
665 degree days to normalise copepodid energy reserves cultured at different temperatures; at 30
666 degree days from hatching, settlement success was 41.6 ± 2.0 % at 20 °C, 53.2 ± 2.3 % at 10
667 °C and 2.1 ± 0.4 % at 5 °C. Key values for infectivity are shown in Table 5.

668 **4.3 Post-attachment variables**

669 A number of variables intervene between initial attachment of the copepodid and successful
670 moulting to the chalimus I stage. In particular, once attached, the copepodid becomes
671 susceptible to host defences, particularly in terms of innate host immunity, often expressed
672 through inflammatory processes. The success of the host response in controlling infection
673 depends upon a number of variables including the species / genotype of the host fish, its age,
674 maturity, health and welfare / stress status and interactions of immune capabilities with
675 environmental parameters such as temperature. The role of the host in mediating infection
676 success will only be covered briefly here as it has been extensively reviewed and investigated
677 by previous authors (Braden *et al.* 2017, Fast 2014, Skugor *et al.* 2008, Tadiso *et al.* 2011 *inter*
678 *alia*). In Atlantic salmon, initial infection by the copepodid can elicit a detectable
679 transcriptomic host response within 1 day post infection (dpi) (Tadiso *et al.* 2011) and some
680 Pacific salmon species, *e.g.* juvenile coho, are able to mount a rapid and successful
681 inflammatory response following infection (Johnson and Albright, 1992; Fast *et al.*, 2002;
682 Jones, 2011) that is capable of killing infecting copepodids within a few days. Atlantic salmon
683 show a less developed inflammatory response and are generally considered to show a poor
684 capacity for removing infecting copepodids (Johnson and Albright, 1992). Despite this
685 observation, different genetic stocks or families of Atlantic salmon can show significant
686 differences in their capacity to resist infection, although the mechanisms underlying
687 differential resistance are currently poorly understood. Jodaa Holm *et al.* (2015) have
688 suggested that differential resistance may reflect the ability of the host to avoid
689 immunosuppression by the parasite. In a comparison of salmon family susceptibility, Gharbi
690 *et al.* (2015) demonstrated a ~60% difference in the median infection count at 7 dpi (chalimus
691 I) for the least and most susceptible salmon families tested by copepodid infection challenge

692 and calculated a genetic heritability of 0.3 for this trait making it a good candidate for selective
693 breeding. The capacity of salmon to reduce infection success may also be modified by extrinsic
694 factors such as diet and temperature. Functional feeds containing a range of active plant or
695 bacterial extracts have, for example, been shown to have significant effects on infection
696 success, providing infection reductions of up to 50% (Jensen *et al.* 2014, Jodaa Holm *et al.*
697 2016, Sutherland *et al.* 2017).

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

706 **5 Mortality through predation**

707 Once sea lice have attached to a host, their chances of survival are increased as they have a
708 constant food supply and external factors affecting survival are relatively few, *e.g.* adverse
709 environmental conditions, host immune response and predation by cleaner fish. During their
710 free-swimming planktonic stages, however, they form a part of a complex plankton food web
711 and are subject to selective and non-selective predation by other plankton and sessile filter
712 feeders such as bivalve molluscs. Global approximations of the partitioning of wider
713 zooplankton mortality suggest that predation accounts for 67–75 % of total mortality in the
714 plankton (Hirst & Kiørboe, 2002). Although predation is likely to have a significant impact
715 on sea lice survival, there are currently no estimates of sea lice predation mortality in the

716 literature due to the difficulty in obtaining this kind of information. Some sea lice dispersion
717 models do include a fixed mortality rate for the free-swimming stages, *e.g.* Amundrud and
718 Murray (2009) used a fixed mortality rate of 0.01 h^{-1} for nauplii and copepodids. Providing an
719 estimate of predation mortality is difficult as plankton assemblages vary considerably
720 according to season and location (*e.g.* Daewel *et al.*, 2014), and prey selection sizes vary
721 amongst the different actively or passively predating species represented in the zooplankton
722 community at any time (Hansen *et al.* 1994; Wirtz, 2011, Wirtz, 2012). As a consequence of
723 a lack of specific data, the following discussion seeks to provide guidance based on wider
724 knowledge of zooplankton, which may be used by researchers to formulate research questions
725 or provide initial parameters for models.

726

727 **5.1 Plankton community structure**

728 In regional marine ecosystems, several processes govern the structure and dynamics of
729 plankton communities. These processes vary according to geographical location, resulting in
730 distinct ocean regions with their own typical plankton assemblages. Small copepods dominate
731 inshore zooplankton with their seasonal abundance following that of the phytoplankton, and
732 clupeid and scombrid fish are the main consumers of pelagic invertebrates (Kaiser, 2005).

733 These broad ocean regions may further be characterised according to ocean processes in
734 different sub-regions, *e.g.* the North Sea, the Norwegian Sea. The abundance of different
735 species that are predators of sea lice larvae and the abundance of other prey will affect the
736 mortality rate of sea lice larvae. Therefore, providing data on larval predation by different
737 plankton assemblages and characterising the plankton assemblage at a specific location
738 represents an important step in predicting mortality rates due to predation.

739 **5.2 Predator selectivity**

740 The body sizes of predator and prey are fundamental in the study of aquatic food webs (Brooks
741 & Dodson, 1965; Woodward *et al.*, 2005). A ‘feeding kernel’ represents a description of the
742 probability of prey ingestion given as a function of feeding rate vs. prey size (Figure 2) (Visser
743 & Fiksen, 2013; Wirtz, 2014). Selective grazing in the presence of a broad spectrum of prey
744 size plays an important role in variable feeding relationships (Sommer & Stibor, 2002), and in
745 the case of larval sea louse predation, the abundance of similar-sized prey must be considered
746 as well as the abundance and size selectivity of predators.

747 Although the relationship between predator and prey body sizes is the primary determinant of
748 grazing selectivity, feeding modes can also affect the size range of plankton selected. Feeding
749 modes can be broadly classified as passive and active ambush feeding, feeding-current feeding
750 and cruise feeding (Kiørboe, 2011), and predators may adjust their feeding behaviour in
751 response to the density of food items, (*e.g.* Kiørboe & Saiz, 1995; Boenigk & Arndt, 2002,
752 Frost, 1972; Visser *et al.*, 2009, Saiz & Kiørboe, 1995). This behavioural plasticity shrinks the
753 overall spectrum of potential prey towards a specific sub-range, and Wirtz (2014) describes
754 two feeding kernels: one for ingestion, which is based on the size range of prey that can be
755 ingested based on biomechanical principles, and one for selection, which describes the actual
756 size range of prey selected according to the availability of prey of various sizes (Figure 2). At
757 high prey densities, many ambush and suspension feeders, such as copepods, typically have a
758 high selectivity resulting in a narrow selection kernel (figure 2a), whereas many facultative,
759 omnivorous feeders, such as jellyfish, typically have broad ingestion and selection kernels
760 (figure 2b) (Wirtz, 2014).

761

762 **5.3 Prey selection**

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

769 Potential predators of sea lice larvae are likely to include obligate and facultative carnivorous
770 zooplankton and planktivorous fish, and given their geographical distribution, predators may
771 be represented by chaetognaths, ctenophores, scyphozoa, euphausiids, mysids and scombrid
772 and clupeid fish. In addition, the larval stages of most fish species rely on copepods as their
773 principal dietary component (Kaiser, 2005).

774 Chaetognaths, or arrow worms, are important predators of copepods and are probably major
775 contributors to the structuring of many marine ecosystems (Steele & Frost, 1977).
776 Chaetognaths are ambush predators, and Fulton (1984) found that active copepods, such as
777 *Acartia tonsa*, decreased in abundance in the presence of *Sagitta hispida*, whereas inactive
778 swimmers, such as *Oithona* spp. did not as encounter rates were lower. As sea lice larvae are
779 active swimmers, it is likely that they will be predated by chaetognaths of a suitable size
780 category.

781 Ctenophores, or comb jellies, are found throughout the world's oceans, and all are predatory,
782 feeding on zooplankton (Fowler, 1911). If food is plentiful, they can eat ten times their own
783 weight per day (Reeve *et al.* 1978). In laboratory experiments, copepodid I larvae of *Calanus*
784 *pacificus* with a mean length of 0.74 mm and mean swimming speed of 0.32 mm s^{-1} , hence
785 similar in size to sea lice larvae, were most susceptible to predation by *P. bachei*, and later
786 juvenile stages, which are larger, were less susceptible to predation (Greene *et al.*, 1986).

787 Scyphozoa, or jellyfish, are generally larger than many other predators in the plankton, and
788 are seasonally common in many coastal environments including those most commonly
789 employed for marine salmonid aquaculture (Doyle *et al.*, 2007). Scyphozoa typically range
790 from 2–40 cm, and their stinging or filter-feeding tentacles enable them to ingest various
791 zooplankton taxa of different sizes, including copepods (Purcell, 1992; Purcell *et al.*, 1994;
792 Suchman & Sullivan, 1998). However, research has shown that scyphozoa are highly
793 selective, and prey size has a significant impact on feeding rates (Suchman & Sullivan, 1998,
794 2000). As scyphozoa are neither visual nor raptorial feeders, they select prey as a consequence
795 of prey vulnerability, and prey with faster swimming speeds and poor escape responses are
796 most vulnerable to predation (Suchman & Sullivan, 2000).

797 Euphausiid and mysid shrimps are two groups of arthropods that are ubiquitous throughout
798 the world's oceans, and due to their high abundance and position in the food chain, they are
799 important components of marine food chains (Båmstedt & Karlson, 1998). While most are
800 omnivorous filter feeders and feed on phytoplankton and detritus, some are carnivorous and
801 feed on other zooplankton (Cripps & Atkinson, 2000). In the Norwegian Sea, the copepod
802 *Calanus finmarchicus* (which has similar-sized juvenile stages to sea lice) is a dominant prey
803 of euphausiid shrimp (Båmstedt & Karlson, 1998).

804 The larval stages of many fish species rely on copepods as their principal dietary component,
805 and although larger gadoids, such as Atlantic cod (*Gadus morhua*) switch to piscivory as
806 adults, smaller species, such as Norway pout (*Trisopterus esmarkii*) and clupeids, such as
807 herring (*Clupea harengus*) remain planktivorous throughout their lives (Daewel *et al.*, 2014).
808 As larval fish are active raptorial predators and rely on sight to detect prey, active prey may
809 be more susceptible to predation. Tiselius & Jonsson (1990) and Doall *et al.* (1998) suggest
810 that the high turn rates of sea lice copepodids during host-seeking behaviour may make them

811 more attractive to predators, such as fish larvae. Some adult fish, such as scombrids and
812 clupeids, feed on plankton throughout their lives, and switch between feeding modes
813 depending on prey density (Janssen, 1976). Zooplankton consumption by fish in the North Sea
814 has been estimated at 19–25 g C m⁻² year⁻¹ of which 28 % of overall zooplankton consumption
815 can be attributed to early life stages of fish (Heath, 2007). In frontal zones, fish larvae could
816 consume up to 3–4 % day⁻¹ of the fraction of preferred zooplankton sizes (Munk *et al.*, 1994).
817 In addition to planktonic predators, sessile feeders, particularly bivalve molluscs and
818 cnidarians, could also have a potential impact on larval sea louse survival. Bivalve molluscs,
819 specifically the blue mussel *Mytilus edulis*, have been suggested to provide efficient clearance
820 of mesoplankton of the same size order as sea lice larvae (Davenport *et al.*, 2000). Only blue
821 mussels and scallops (*Placopecten magellanicus*) have been specifically investigated in terms
822 of their ability to clear larval sea lice (Molloy *et al.*, 2011, Bartsch *et al.*, 2013). Molloy *et al.*
823 (2011) demonstrated that mussels were capable of removing copepodids from the water
824 column under experimental conditions and this was also demonstrated by Bartsch *et al.* (2013)
825 who showed that mussels and scallops could remove 18–38 % of presented copepodids per
826 hour. While it has been suggested that mussels or other bivalves might, therefore, be employed
827 to help control sea lice on farms (Molloy *et al.*, 2011, Bartsch *et al.*, 2013), it has been noted
828 (Bravo, pers. comm.) that close proximity of mussel farms and salmon farms in Chile has not
829 served to reduce apparent levels of sea lice infections.

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

833

834 **6 Research gaps identified, recommendations and conclusions**

835 A broad range of factors impact the levels of egg production by host-attached lice and the
836 subsequent proportion of the initial extruded egg number that go on to successfully infect fish
837 as copepodid larvae. Figure 3 shows the stages of the sea louse life cycle that determine the
838 number of copepodids available for infection and their infection success and summarises the
839 factors reviewed in this study that may affect subsequent levels of infection.

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

$$843 \quad S = EP_hP_pP_dP_sP_eI$$

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

855 By forming a table of these variables and the observable factors that may influence them
856 (Table 6), it is clear that there are a considerable number of permutations, each requiring
857 observational data to allow variables to be fully defined. While a number of these variables
858 have been previously investigated, as described in this review, a lack of data for some variables

859 results in an incomplete dataset (Table 6). Furthermore, a lack of standardisation and
860 consistency across different studies due to various experimental conditions and the origin of
861 experimental lice, *e.g.* of Atlantic or Pacific origin, farmed or wild origin, cold-adapted or not,
862 means that many data points are not directly comparable. In addition, some studies are based
863 on laboratory experiments conducted under controlled conditions, whereas others are based
864 on field data. Gravid (1996) recorded the widths of nauplius I larvae and the lipid reserves from
865 field-collected lice at different times of year, and although no other studies considered seasonal
866 variations in their experiments *per se* (Table 6), seasonal variation subsumes a number of
867 observable/observed factors, such as temperature, photoperiod and salinity, and other factors
868 that are not considered here, such as host condition and plankton assemblages.

869

870 **6.1 Key gaps in knowledge identified**

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

875

876 **6.1.1 Egg production (E), egg viability and hatching success (P_h)**

877 Previous estimates of egg production in the literature vary across more than an order of
878 magnitude, are relatively inconsistent and are incomplete in their coverage of relevant factors.
879 As this is the key input variable driving subsequent modelled infection levels, better estimates
880 of production are an obvious priority. In addition to this, it is clear from the relatively sparse

881 earlier studies that have been conducted that egg viability and hatching success are rarely, if
882 ever, 100 % and can be substantially lower than this according to a range of factors (Table 2).

883 Egg production level is influenced by a broad range of factors including temperature (and
884 temperature adaptation), salinity, host state (nutrition, immunity, stress, species, genotype),
885 egg batch and others. For this reason, it will be extremely difficult to establish realistic values
886 through tightly controlled laboratory experiments alone. Egg production can, however, easily
887 be established through a programme of farm sampling over a year, with counts of eggs per
888 millimetre and the measurement of egg string lengths being conducted on-farm using a
889 stereomicroscope or in the laboratory following sample preservation. Laboratory analysis
890 could also employ image analysis to increase accuracy and sample throughput. During the
891 sampling period, the recording of farm metadata, such as temperature, salinity, salmon stock,
892 feed source, treatment regime *etc.*, would allow an accurate and informative predictive model
893 to be produced. In order to give a better picture of total egg production, samples from wild
894 salmonids would also be helpful as it is well-recognised that egg strings sourced from lice on
895 wild fish tend to have higher numbers of eggs (Tully & Whelan, 1993; Pike & Wadsworth,
896 1999).

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

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

903

904 **6.1.2 Predation in plankton (P_p)**

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

911 Even with good estimates of larval production, the fate of larvae in the plankton is a key
912 mediator of numbers available to infect fish. Plankton studies are notoriously difficult and are
913 not easily amenable to laboratory-based experiments. To achieve estimates of mortality in
914 plankton, mesocosm studies offer the best approach, whereby in different seasons local
915 plankton are enclosed in a mesocosm, and a known number of larval sea lice are introduced to
916 the system. Following a period to allow for predation, the filtering of the mesocosm will allow
917 estimations of plankton types/species present and the clearance rates of sea louse larvae. The
918 use of molecular tools might also allow an investigation of the major predators in any given
919 plankton sample.

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

923

924 **6.1.3 Infectivity profile (I)**

925 To date, there has been a tendency to equate the number of copepodids in the water column
926 with the number of infecting individuals. From previous observations, however, it is apparent
927 that there is a profile of infectivity, *i.e.* the ability of lice encountering a fish to infect it as they

928 age, with newly moulted individuals being less infective than those having matured for 1–2
929 days and a subsequent decline of infectivity towards death. Infection success requires
930 definition as not all copepodids that attach to a host may establish a successful infection; the
931 number of copepodids developing to the chalimus I stage and developing a permanent
932 attachment via a frontal filament may be an appropriate measure of infection success. Even
933 under the optimal conditions of an experimental infection challenge, the infective success of
934 maximally infective copepodids is rarely higher than 50 % and is frequently lower. From the
935 literature, few researchers have attempted to establish infection profiles for cohorts of
936 copepodids under different conditions of, for example, temperature, salinity and current speed,
937 despite clear evidence that these factors will all affect infection success. Most challenge
938 experiments employ static tanks and long exposure times, providing a totally inaccurate
939 reflection of probabilities for real-world infection success.

940 While the infectivity profile needs to be better established under laboratory conditions, these
941 will not fully reflect field conditions but will tend to provide an overestimate of infection
942 success rate. Using standard tank challenges it is possible to profile the infectivity of
943 copepodids with age and under different temperature and salinity conditions. However, a more
944 accurate reflection of infectivity can be achieved using flume experiments where fish are
945 exposed to copepodids under current flow conditions more reflective of field conditions.

946 One important source of potentially valuable data concerning losses incurred between egg
947 hatching and the reinfection of hosts is the detailed farm louse counts already conducted in
948 many countries. Assuming knowledge of seasonal levels of egg production and viability,
949 which may be easily obtained, the annual profile of copepodid/chalimus counts, can, at least
950 for some more hydrographically constrained regions, provide an indication of the proportion
951 of hatched larvae that successfully re-establish infections on fish.

952

953 **6.2 Co-ordinated research**

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

960

961 **6.3 Conclusions**

962 The estimation of lice burdens on wild and cultured fish can inform the timing of pest
963 management decisions in salmonid aquaculture. In the life cycle of the sea louse, egg
964 production, survival of free-swimming stages and infectivity of survivors are key determinants
965 of the number of lice re-establishing host infection. Despite several decades of research,
966 however, knowledge of this area of sea louse biology is lacking, which confounds the accurate
967 estimation of lice infections using epidemiological modelling. Even where parameters have
968 been measured by researchers, the wide variety of data sources and experimental approaches
969 employed, limits the possibility of providing ‘best’ or consensus values for use in modelling.
970 With further research of the key variables that affect the production and survival of free-
971 swimming larval sea lice, it should be possible to more accurately model the production and
972 dispersal of lice from cage aquaculture and wild fish, which will inform the optimum timing
973 of pest management procedures. Furthermore, with an improved knowledge of larval sea louse
974 mortality, it may be possible to incorporate natural processes into management decisions and
975 to manage timing of treatments appropriately, *e.g.* reflecting larval predation following spring

976 algal blooms. While many aspects of louse biology are important in determining the numbers
977 of lice available for infection, care should be taken to avoid the over-parameterisation of sea
978 louse infection models. The identification of the key variables from the complex biology of
979 sea lice that have the greatest impact on their numbers can be achieved through a sensitivity
980 analysis of model parameters. Accurate predictions of sea lice infections are a single
981 component of integrated pest management protocols, and when used in conjunction with the
982 continuous monitoring of lice populations on farmed fish and effective treatment procedures,
983 it should be possible to minimise the environmental and economic impact of these pathogens
984 on farmed and wild salmonids.

985 *7 Acknowledgements*

986 This study was funded by a Scottish Aquaculture Research Forum grant (SARF108). The
987 authors would like to thank Dr Darren Green for guidance on mathematical modelling.

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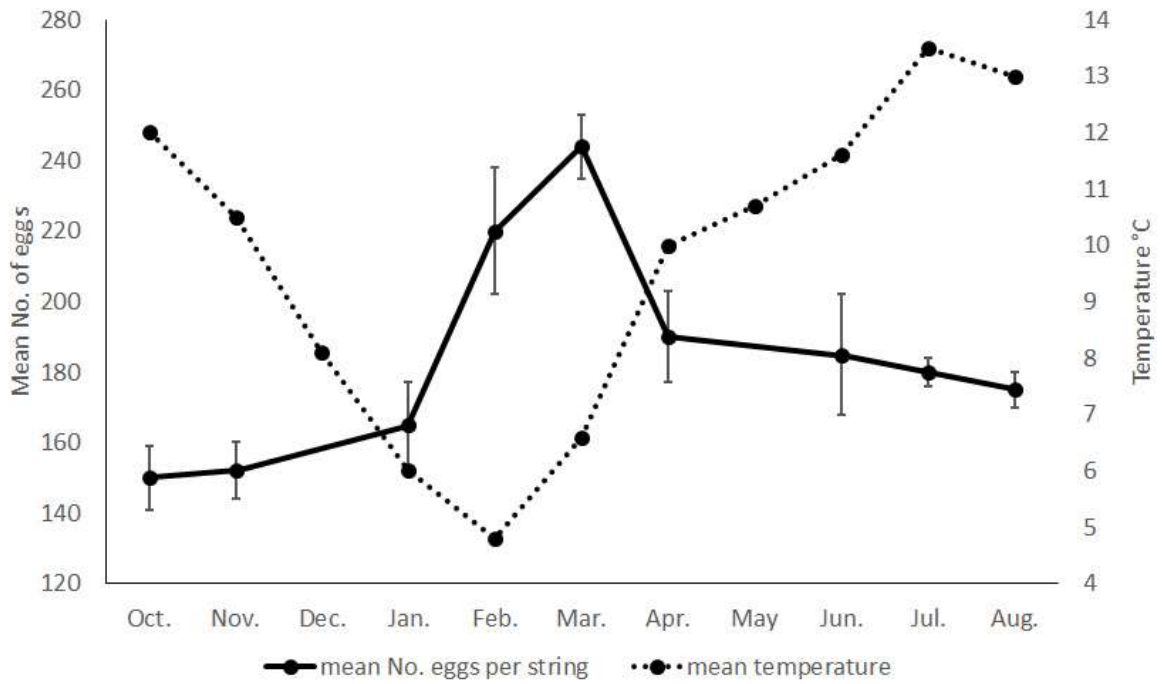
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1405

1406 **9 List of Figures**



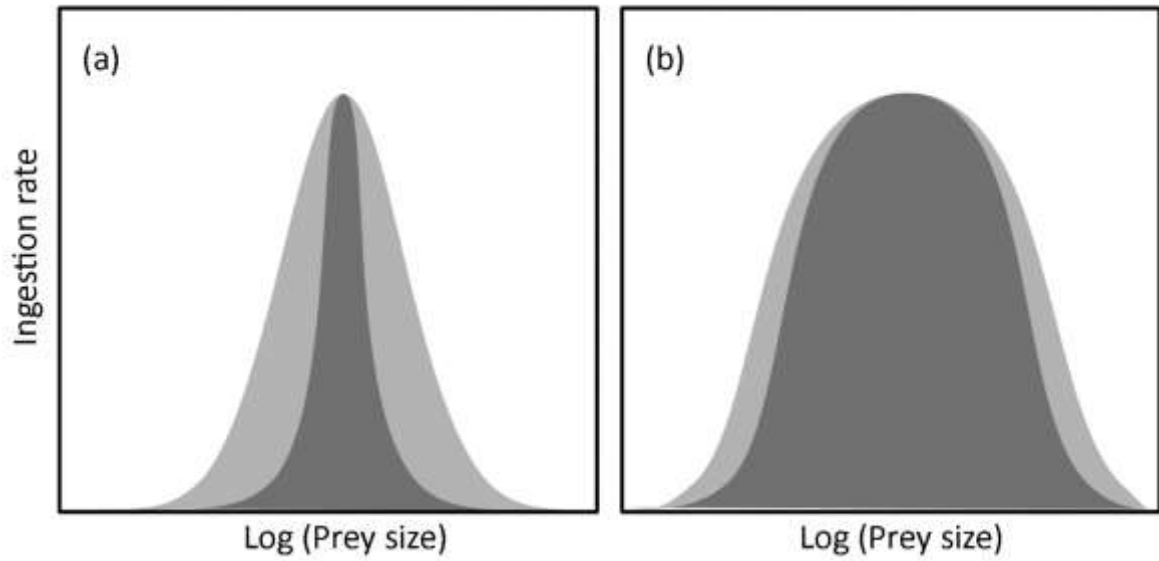
1407

1408 **Figure 1.** Relationship between water temperature and the number of eggs per egg string in
1409 *Lepeophtheirus salmonis* from salmon farms on the West Coast of Scotland. Redrawn from
1410 Ritchie *et al.*, 1993

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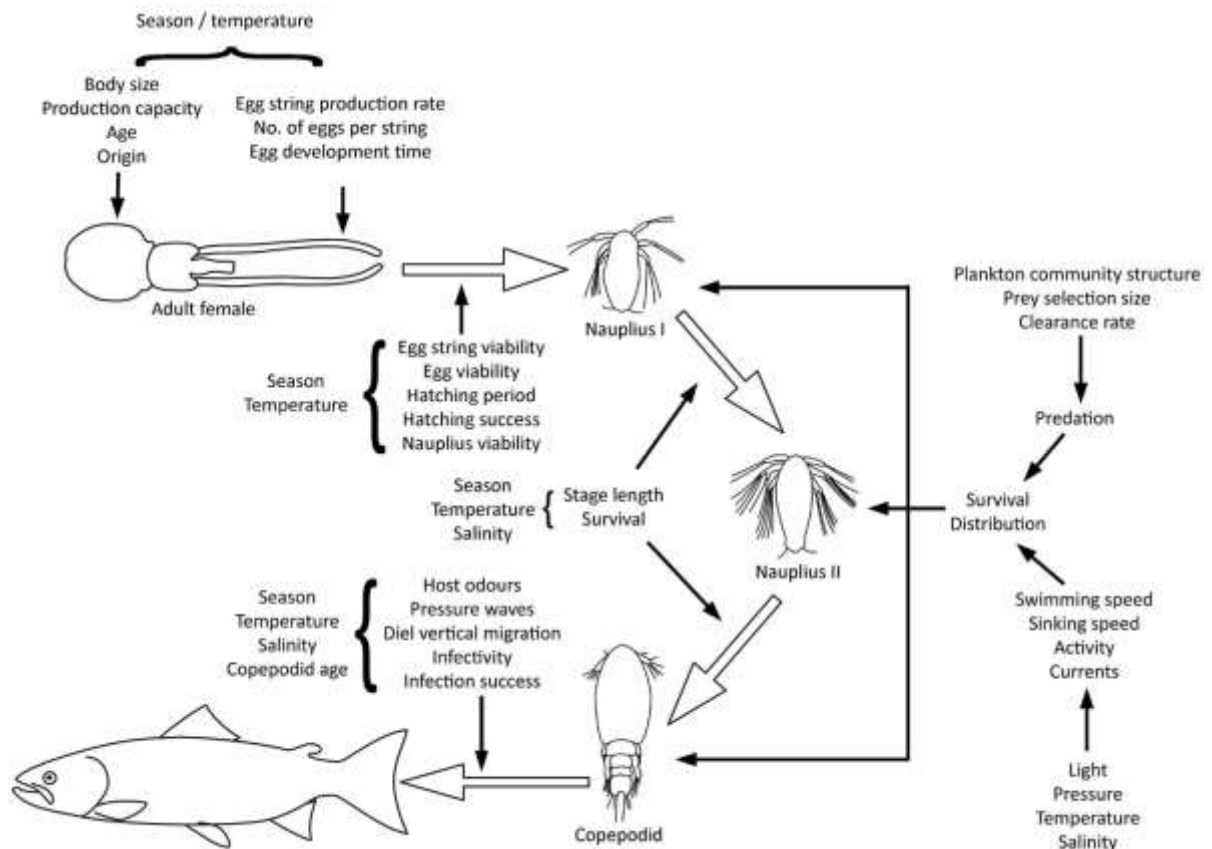


1414

1415 **Figure 2.** Typical ingestion (light grey area) and selection (dark grey area) feeding kernels for
 1416 (a) narrow-range, selective feeders, *e.g.* copepods, and (b) broad-range, unselective feeders,
 1417 *e.g.* jellyfish, where prey are abundant. Adapted and redrawn from Wirtz (2014)

1418

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1420

1421 **Figure 3.** A conceptual model of the stages of the sea louse life cycle that determine the
 1422 number of copepodids available for infection and their infection success with factors that may
 1423 affect survival/infectivity at each stage. Open arrows show the life cycle and black arrows
 1424 show the factors that may affect each stage of the life cycle.

1425 **10 List of Tables**

1426 **Table 1.** Key values of fecundity in *L. salmonis* (means \pm SD). References: (a) Heuch *et al.*, 2000, (b) Johnson & Albright, 1991b, (c) Gravid,
 1427 1996, (d) Pike & Wadsworth, 1999, nd = no data available.

	<i>L. salmonis salmonis</i>			<i>L. salmonis oncorhynchi</i>		
	Time (d)	Egg string pairs	No. of eggs	Time (d)	Egg string pairs	No. of eggs
<i>Egg string production rate</i>						
7.2 °C	11 ^a	-	-	nd	-	-
12.2 °C	5 ^a	-	-	nd	-	-
<i>Production capacity</i>	-	4.95 ^a	-	-	nd	-
<i>No. egg strings per string</i>						
7.2 °C	-	-	1st string 152 subsequent strings 285 ^a	-	-	nd
10 °C	-	-	nd	-	-	344.6 \pm 79.8 ^b
1 st string	-	-	141.09 \pm 22.19 ^c	-	-	nd
2 nd string	-	-	216.4 \pm 67.59 ^c	-	-	nd
3 rd string	-	-	208.2 \pm 50.97 ^c	-	-	nd
wild lice	-	-	965 \pm 30.1 ^d	-	-	nd
farmed untreated lice	-	-	758 \pm 39.4 ^d	-	-	nd
farmed treated lice	-	-	297 \pm 19.1 ^d	-	-	nd

1428

1429 **Table 2.** Key values of hatching in *L. salmonis*. (Means \pm SD, parentheses indicate ranges).

1430 References: (a) Gravid, 1996, (b) Heuch *et al.*, 2000, (c) Johnson & Albright, 1991b, (d)

1431 Samsing *et al.*, 2016, nd = no data available.

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

1432

1433 **Table 3.** Key stage timings for *L. salmonis* (mean values). References: (a) Johnson & Albright,
 1434 1991b, (b) Johannessen, 1977, (c) Wootten *et al.*, 1982, (d) Gravid, 1996, (e) Boxaspen & Næss,
 1435 2000, (f) Samsing *et al.*, 2016, nd = no data available.

	<i>L. salmonis salmonis</i>		<i>L. salmonis oncorhynchi</i>	
	Time (d)	Time (h)	Time (d)	Time (h)
<i>Egg development time</i>				
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	-
<i>Duration of first nauplius stage</i>				
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
<i>Duration of second nauplius stage</i>				
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
<i>Development time to copepodid</i>				
2 °C	-	1644 ^e	-	nd
5 °C	-	276 ^f	-	nd

7 °C	-	168 ^f	-	nd
10 °C	-	111–177.5 ^d	-	nd
		305 ^e		
		108 ^f		
15 °C	-	36 ^f	-	nd
20 °C	-	48 ^f	-	nd

1436

1437 **Table 4.** Key values of survival for *L. salmonis* larvae (50 % survival times (LT₅₀) are shown
 1438 unless specified otherwise). References: (a) Gravid, 1996, (b) Johnson & Albright, 1991b, (c)
 1439 Bricknell *et al.*, 2006, (d) Wootten *et al.*, 1982, (e) Samsing *et al.*, 2016, nd = no data available.

	<i>L. salmonis salmonis</i>			<i>L. salmonis oncorhynchi</i>		
	width(µm)	Proportion	Time (h)	width (µm)	Proportion	Time (h)
<i>Nauplius I width</i>						
May	187.76 ^a	-	-	nd	-	-
August	214.05 ^a	-	-	nd	-	-
<i>Nauplius I lipid reserve width</i>						
May	112.98 ^a	-	-	nd	-	-
August	135.84 ^a	-	-	nd	-	-
<i>Survival to copepodid at 10 °C</i>						
<25 ppt	-	0% ^a	-	-	nd	-
<30 ppt	-	nd	-	-	0% ^b	-
30 ppt	-	nd	-	-	35.2% ^b	-
35 ppt	-	18.33% ^a	-	-	nd	-
<i>Copepodid survival time at 10 °C</i>						
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
<hr/>						
<i>Copepodid survival time at 35 ppt</i>						
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

1440

1441 **Table 5.** Key variables of infectivity in *L. salmonis salmonis* larvae. References: (a) Cook *et*
1442 *al.*, 2010, (b) Bron, 1993, (c) Gravid, 1996, (d) Tucker *et al.*, 2002, (e) Samsing *et al.*, 2016, (f)
1443 Bricknell *et al.*, 2006. No infectivity data is available for *L. salmonis oncorhynchi*.

	Infectivity capability	Lipid reserves	Proportion
<i>Copepodid age</i>			
7–10d	Increasing ^{abcd}	Good ^{abcd}	-
11–15d	Mature ^{abcd}	Decreasing ^{abcd}	-
16–20d	Less capable ^{abcd}	Low ^{abcd}	-
<hr/>			
<i>Infection success at 10 °C and 35 ppt</i>			
1-day-old copepodids	-	-	22.22 ± 8.32% ^c
7-day-old copepodids	-	-	14 ± 8.71% ^c
<hr/>			
<i>Infection success aged 1–3 d</i>			
Illumination	-	-	23.2% ^b
No illumination	-	-	18.4% ^b
<hr/>			
<i>Infection success at 35 ppt</i>			
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

1444

1445 **Table 6.** A summary table of parameters influencing the production, timing and survival of
 1446 sea lice larvae and observable biotic and abiotic factors that may influence them. Cells
 1447 marked with an X represent areas where some data already exist and blank cells represent
 1448 areas of data deficiency. References: (a) Heuch *et al.*, 2000, (b) Tully & Whelan, 1993, (c)
 1449 Gravil, 1996, (d) Ritchie *et al.*, 1993, (e) Johnson & Albright, 1991a, (f) Tully, 1992, (g)
 1450 Samsing *et al.*, 2016, (h) Johnson & Albright, 1991b, (i) Johannessen, 1977, (j) Boxaspen &
 1451 Næss, 2000, (k) Wootten *et al.*, 1982.

Parameter	Origin: wild / farmed	Variable factor			Reference
		Temp.	salinity	Light / photoperiod	
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

1452