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A method of estimating *in situ* salmon louse nauplii production at fish farms

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ABSTRACT: Abundance and depth distribution of planktonic sea lice were investigated in relation to hydrodynamics and diurnal solar insolation at a salmon farm in Sundalagið, Faroe Islands. Plankton surveys were conducted by surface tows with a plankton net around the farm and by using a plankton pump at 1, 4 and 6 m depth in a fish cage. The entire sample content was investigated under a stereomicroscope and sea lice were identified. Sea lice of the species *Lepeophtheirus salmonis* and *Caligus elongatus* were present at the farm. Nauplii dominated the planktonic stages (>95%) while copepodids were absent from most samples. The highest observed copepodid density was 0.3 ind. m^{-3}, which is within the range found in open water. No diurnal vertical distribution pattern was observed for salmon lice nauplii in the net cages, which were most abundant in the top meter of the water column, and density decreased with depth. At 1 m depth, nauplii density was inversely proportional to the current speed at the same depth. From this relation, and the abundance of adult female sea lice on the farmed fish, the *in situ* nauplii production was calculated to be within 26–68 nauplii $female^{-1}$ d^{-1}. The lower end of this range is similar to production rates suggested by laboratory studies at similar temperatures (7.8°C).

KEY WORDS: *Lepeophtheirus salmonis* · *Caligus elongatus* · Sea lice · Infectious copepodid · Nauplii · Sea cage farming · Aquaculture · Salmon louse

INTRODUCTION

The salmon louse *Lepeophtheirus salmonis* is a naturally occurring parasitic copepod in the northern hemisphere and has been a subject in the salmon farming industry since the onset of commercial salmon aquaculture (Pike & Wadsworth 1999). Typically, salmonids are farmed in floating net pens with free water exchange. This ensures removal of waste and supply of oxygenated water. However, the free water exchange also includes exchange of pathogens such as salmon lice, which transmit between hosts as planktonic larvae (Pert et al. 2014). In addition to *L. salmonis,* salmon farmed in the North Atlantic Ocean may also be infected by the teleost generalist *Caligus elngatus* (Nordmann, 1832). However, as *L. salmonis* is more pathogenic to farmed salmon, it has been studied more intensively than *C. elongatus* (Boxaspen 2006).

Both species have 3 planktonic stages; 2 nauplius stages prior to the infective copepodid. Both nauplii and copepodids are non-feeding and drift with the currents (Pike & Wadsworth 1999, Boxaspen 2006). However, they show behavioural traits that play a role in host-finding (Mordue & Birkett 2009), and they also respond to environmental stimuli; e.g. avoidance of freshwater (Bricknell et al. 2006), diel vertical migration (Heuch et al. 1995) and recently, the likelihood of nauplii vertically seeking the highest possible temperature has been discussed (Johnsen et al. 2014, á Norði et al. 2015).

Salmon farms are identified as contributors to the salmon lice infection pressure of both farmed and wild salmonids (Morton et al. 2011, Aldrin et al. 2013, Serra-Llinares et al. 2014, 2016). This is especially the case towards the end of the farming cycle, when the prevalence of adult female lice on the farmed fish can be high (Torrissen et al. 2013). There are numer-

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ous estimates and models of the infection pressure from farmed fish that are based on the amount of gravid female sea lice on the fish, laboratory trials and wind and current conditions (Heuch & Mo 2001, Orr 2007, Serra-Llinares et al. 2014). However, to our knowledge, *in situ* observations of production and survival of nauplii have not been accomplished.

In spite of the persistent presence of salmon lice, the production of farmed salmon has increased continuously since the onset of farming (FAO 2014). The use of chemotherapeutics has played an essential role in keeping the sea lice levels on farmed fish below sub-clinical levels, and in the mitigation of pathogen transmission between farmed and wild populations. However, the development of resistance to chemotherapeutics in salmon lice populations (Aaen et al. 2015) has called for sea lice control mechanisms other than chemical agents.

Various technologies that aim to prevent the infectious copepodids from reaching the farmed fish e.g. shielding skirts, snorkel cages, underwater feeding and light, light traps, electric fences and mussel beds are under development or have been developed (Molloy et al. 2011, Frenzl et al. 2014, Lien et al. 2014, Aaen et al. 2015). The majority of these technologies are based on the copepodids being most abundant in the upper few meters of the water column (McKibben & Hay 2004, Penston et al. 2004, Molinet et al. 2011), and responding to light stimuli (Hevrøy et al. 2003, Genna et al. 2005). However, observations on the target organism around fish farms are quite limited, and basic information is still scarce.

To our knowledge, planktonic salmon lice have been sampled inside net pens in 2 studies (Costelloe et al. 1996, Gravil 1996), whereas studies of sea lice larvae at distances to fish farms are more numerous (Costelloe 1998, McKibben & Hay 2004, Penston et al. 2004, 2008, 2011, Penston & Davies 2009, Molinet et al. 2011, Morton et al. 2011, á Norði et al. 2015)

In the vicinity of fish farms, *L. salmonis* nauplii are the most common developmental stage found, while observations of copepodids are scarce (Costelloe et al. 1996, Morton et al. 2011). The nauplii-to-copepodid ratio decreases with distance to the farms, due to a decrease in nauplii density (Costelloe et al. 1996). Highest copepodid densities are commonly observed in near-shore environments, ideal for intercepting migrating hosts (Costello 2006). This is most probably a result of the copepodids drifting with the surface currents influenced by wind (Salama & Rabe 2013, Asplin et al. 2014, á Norði et al. 2015).

In this paper, 2 snapshots of sea lice abundance at a fish farm are presented in relation to the concurrent hydrodynamics, solar insulation and sea lice counts on the farmed fish. Further, it is demonstrated how an *in situ* estimate on the nauplii production can be accomplished from such high-resolution measurements.

MATERIALS AND METHODS

Study site

The study was conducted at a fish farm in the northern part of Sundalagið, Faroe Islands, towards the end of the farming cycle when sea lice prevalence on farmed fish was at its maximum. The farm consisted of 18 net cages mounted below a floating platform in arrays of 3 × 6 (Fig. 1). The dimensions of the net cages were 24 × 24 × 20 m. No artificial light source was applied at the farm, and an automatic feed dispenser continuously fed the fish at the surface during daylight. Surface water temperature and salinity ranges in the area are quite small, ranging from 6 to 11°C and 32 to 35, respectively (Gaard et al. 2011, á Norði et al. 2015). No sharp pycnocline, but a gradual change in salinity and temperature with depth occurs in the upper 20 m due to wind-induced mixing (á Norði et al. 2015).

A spatial and a temporal survey of sea lice distribution were conducted. First, on February 7, 2014 the spatial distribution of sea lice was investigated at 1 m depth at 14 different sites inside and around the fish farm (Fig. 1). Samples were taken in daylight within 5 h at the time when the fish farm was at the end of the grow-out period and held 675 000 salmon.

The second survey investigated temporal changes in sea lice abundance in one of the net cages at the farm. Plankton samples were consecutively taken at 1, 4 and 6 m depth every third hour over a 24 h period. The survey began on May 6, 2014, at which time harvesting had commenced with net cage and adjacent cages being in full production. The investigated net cage held 35 000 salmon. During the measurements, the solar insulation was recorded hourly with a digital Quantum Scalar Laboratory sensor (QSL – 2100, Biopsherical Instruments).

During both surveys, temperature, salinity and water current measurements were performed adjacent to the cages for 24 h at 1 m depth with a Seaguard RCM SW from Aanderaa (www.aanderaa.com). In order to collect information on the water current field around the farm, the deployments were conducted on diagonal corners at the farm. The net cages were virtually without biofouling, as observed by an underwater camera.

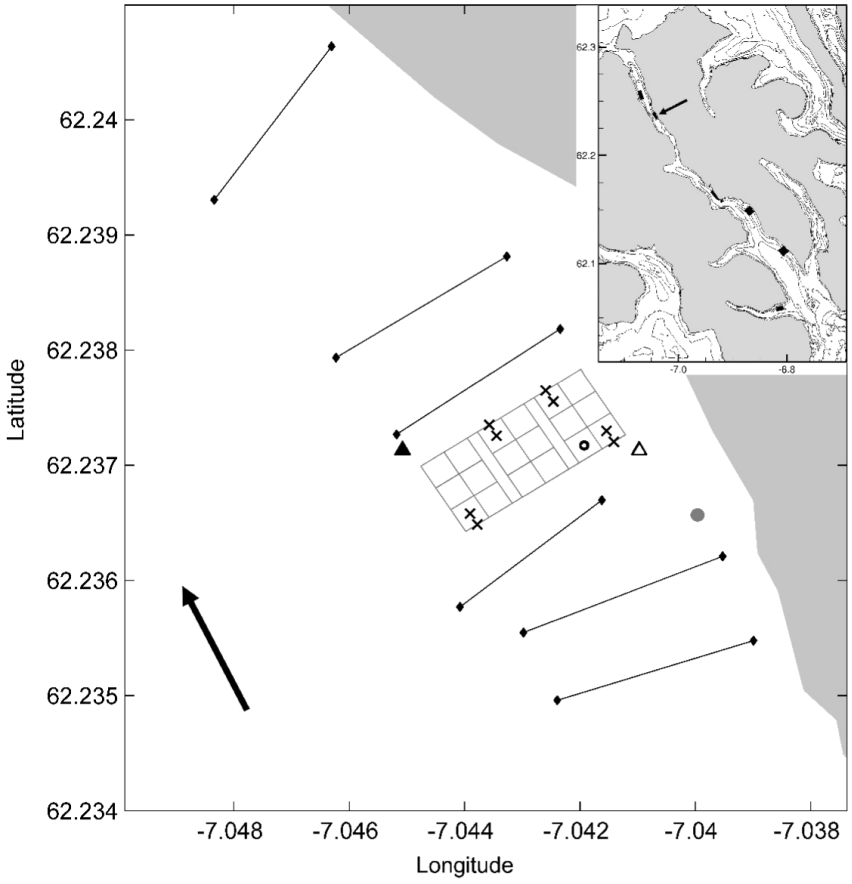

Fig. 1. Location of sampling stations and the fish farm in Sundalagið strait (~38 km long), Faroe Islands. At the farm, plankton was sampled by a plankton pump at 1, 4, and 6 m depth in the temporal study (position indicated by ○), and at 1 m depth in the spatial survey (positions indicated by +). Around the farm, samples were taken by towing a plankton net ~180 m parallel to the farm (black lines with diamonds, just below the surface. The triangles outside the farm show the locations of the current meter at the spatial (▲) and the temporal (△) survey, and the arrow indicates the main current direction at the positions of the current measurements. The position and size of the feed barge is shown in grey. Inset: Location of the study area in relation to Sundalagið. Fish farming areas are shown as black areas, and an arrow points to the studied farming area

Planktonic sea lice

Inside the cages and outside the walkway of the floating platform, plankton was sampled by a plankton pump model 23.570 (KC-Denmark) with a mesh size of 150 µm and a capacity of 300 l min^{-1}, from 0 to 40 m depth. The volume of filtered seawater was calculated from the pump time and capacity. A mesh size of 150 µm is commonly applied in plankton surveys on sea lice abundance (Costelloe 1998, McKibben & Hay 2004, Penston et al. 2004, 2008, 2011, Molinet et al. 2011).

For the spatial survey, a fittered volume of 4.5 m^3 was chosen, as previous studies inside fish cages suggested this to be sufficient (Costelloe et al. 1996, Gravil 1996). However, for the temporal study, the volume was increased to 6 m^3, which was close to the maximum volume that is applicable in order to investigate samples at 3 depths every third hour, given the capacity of the plankton pump.

The intake of the pump was held at the selected depths by floats. Inside the net cages, samples were taken near the center of the 24 × 24 m cages while samples outside the cages were taken ~2 m outside the net (Fig. 1).

At distances from 40 to 340 m up- and downstream the farm (Fig. 1), plankton samples were obtained with a 150 µm mesh size plankton net. The mouth diameter was 50 cm, and the uppermost part of the mouth was held at ~25 cm depth by floats and weights. The net was towed for 180 ± 10 m parallel to the fish cages by a fish farm catamaran at a constant speed of 0.8 m s^{-1}. The location and length of the tows was recorded with a hand-held GPS (GPSmap 62s, Garmin). The feed pipes and feed barge positioned south of the farm, however, made it unfeasible to mirror the sampling distances north and south of the farm. Samples were preserved in ethanol (99.9%) and counted within 5 d after sampling. The entire sample content was analysed using a stereomicroscope, and the nauplii and copepodids were identified by their morphometrics and pigmentation pattern and colour (Schram 2004).

Sea lice on farmed fish

Data on the farmed fish and on the abundance of adult *Lepeophtheirus salmonis* females and gravid *Caligus elongatus* present on the fish were provided by the fish farming company. The sea lice data was obtained from legislated sea lice monitoring, counting sea lice on 10 fish in each of 4 cages fortnightly. *L. salmonis* were grouped into preadults plus males and adult females with or without egg strings. *C. elongatus* were grouped into adults and gravid females.

Statistical analysis

The relationship between current speed and nauplii abundance at 1 m depth, and the nauplii depth distribution were investigated by general linear models with the statistical software package R (www.r-project.org). An exponential decrease in nauplii abundance as a function of depth was chosen, as the R^2 values of tested relationships suggested this to be the best fit. Thus, the nauplii abundance was log transformed prior to analysis by the general linear model. For the analysis of the nauplii abundance dependency on current speed, an invert linear relation with fixed intercept was used.

RESULTS

Hydrography

The current direction at 1 m depth at the fish farm was continuously northwards along the sound with the current speed changing with the semidiurnal tides (Fig. 2). In February the range in current speed measured approximately 240 m from the coast was 0.02 to 0.24 m s^{-1}, while in May the current measured ~70 m from the coast ranged from 0.02 to 0.12 m s^{-1}. Both records were conducted about 2 d before a neap tide of approximately the same strength. Thus, the difference in measured current speed is likely due to a gradient in current speed with distance from the coast.

Spatial distribution of sea lice

At the spatial survey in February, sea lice of the species *Lepeophtheirus salmonis* and *Caligus elongatus* were present in the plankton samples (Fig. 3). *C. elongatus* was the dominant species, with the *C. elongatus* to *L. salmonis* ratio being 2.7:1. The abundance of *L. salmonis* was low, and in the samples at the fish farm, the numbers ranged between 0 and 2 only. Thus, the sea lice abundance at the farm is presented as an average of the 4 cages (Fig. 3).

Nauplii dominated the planktonic stages with 95% of the observed sea lice. For both species, nauplii occurred sporadically upstream of the farm, while highest density was found within 125 m downstream (Fig. 3). The maximum *L. salmonis* density of 0.37 ind. m^{-3} was 40 m downstream, and maximum *C. elongatus* density was 1.1 ind. m^{-3} observed 125 m downstream. At the station 340 m downstream of the farm, nauplii density of both species was <0.06 ind. m^{-3}, although at least 2/3 of the tow was in the direct wake of the farm, as measured by the current direction. At the fish farm, the *L. salmonis* nauplii abundance varied between 0 and 0.4 ind. m^{-3} while the *C. elongatus* abundance varied between 0 and 1.1 ind. m^{-3}. In samples taken just outside the walkways of the platform, *L. salmonis* and *C. elongatus* nauplii were present in the 2 samples downstream of the cages, while no nauplii were found upstream.

Salmon lice copepodids were only observed in one sample upstream of the farm, and in a net cage. *C. elongatus* copepodids were observed in and around cages and in a sample downstream of the farm (Fig. 3).

The 24 h averaged surface water temperature was 6.3°C, and the average number of adult *L. salmonis* females per farmed fish was 1.6, while the average number of gravid *C. elongatus* was 2.7, as observed in the sea lice monitoring conducted 3 d after the present study.

Temporal abundance of sea lice

No planktonic *C. elongatus* were found during the temporal survey in May; all the sea lice were *L. salmonis*. As for the spatial survey, the bulk was nauplii (98%).

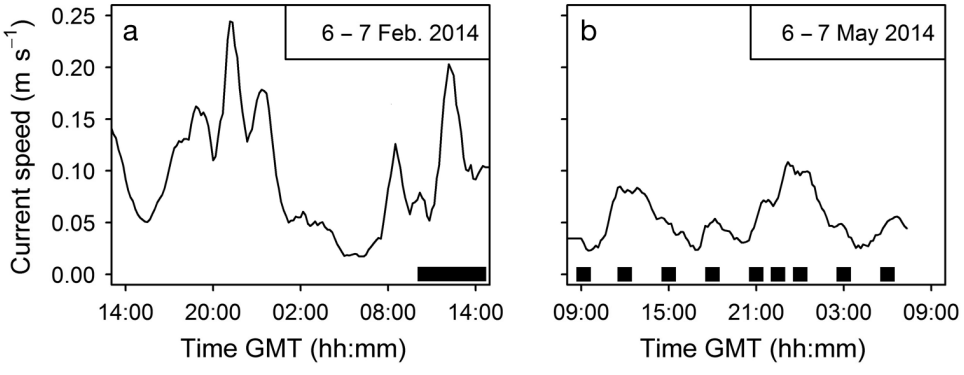

Fig. 2. Current speed (smoothed 1 h running average) at 1 m depth at (a) the spatial and (b) the temporal survey sites. The current meter was closer to the shore at the temporal survey site (see Fig. 1). The black bar in (a) denotes the sampling period for the spatial sampling, and black squares in (b) represent the tim-

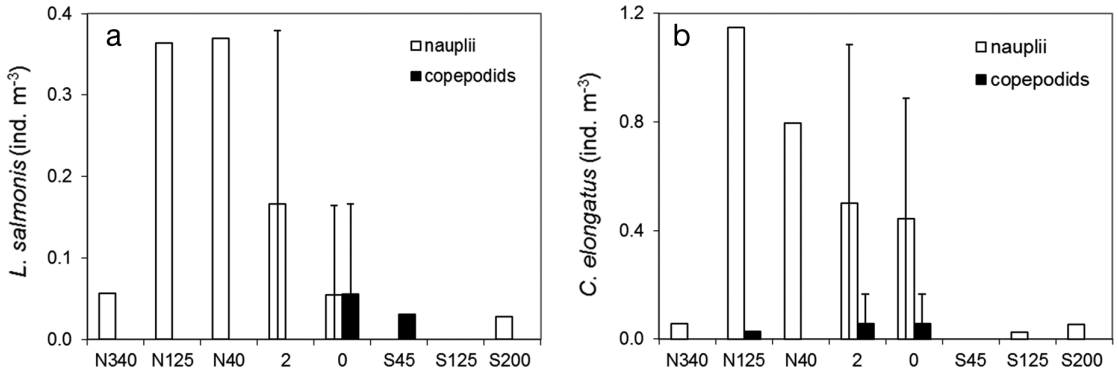

Fig. 3. Abundance of (a) *Lepeophtheirus salmonis* and (b) *Caligus elongatus* at various distances downstream (N) and upstream (S) of the fish farm. The numbers denote the distance from the farm (in m). Open bars: nauplii, closed bars: copepodids. Values for measurements at 0 m (center of fish cages) and 2 m distance (outside fish cages) are mean ± SE of 4 samples conducted at 1 m depth with a plankton pump, while values at greater distances are from single surface tows with a plankton net (Fig. 1)

The density of *L. salmonis* nauplii in the investigated net cage was considerably higher than the density observed in the spatial survey. *L. salmonis* nauplii were present in all but one of the 25 samples, with densities of up to 4.2 nauplii m^{-3} (Fig. 4). The average number of adult *L. salmonis* females on individual farmed fish was 1.3, which was somewhat lower than in the spatial survey, and the surface water temperature had increased to 7.8°C. The number of sea lice may vary between cages, and at the investigated farm the variation increased towards the end of the farming cycle as observed in sea lice monitoring data. Based on the between-cage variation in sea lice numbers in the monitoring programme, the number of adult *L. salmonis* females in the investigated fish cage ranged from 0.71 to 1.85 (95% confidence interval).

Copepodids were observed in 5 samples. The limited number of observations did not reveal any diurnal pattern in copepodid appearance as they were observed in 2 samples carried out in daylight and 3 during the night, nor was any vertical distribution pattern observed.

The depth-distributed nauplii abundance did not change with solar radiation (Fig. 4). The nauplii abundance rather showed a semidiurnal pattern, which was most pronounced at 1 m depth. The greatest variation, as well as highest mean nauplii density, was observed at this depth (Fig. 5). Mean nauplii abundance decreased exponentially with depth (Fig. 5). The exponential fitted plot ($R^2 = 0.9994$, $p < 0.05$) from the surface to the bottom of the cage shows a range in mean nauplii abundance from 2.5 naupl. m^{-3} at the surface to 0.3 naupl. m^{-3} at 10 m depth, and that 73% of the nauplii were located in the upper 6 m of the water column.

The semidiurnal variation in current speed (Fig. 2) and nauplii abundance (Fig. 4) indicates a dependency between the two, and there was an inverse relation between the current speed perpendicular to the cage and the nauplii abundance at 1 m depth (Fig. 6).

DISCUSSION

Observations of copepodids in association with the fish farm were scarce. They were absent from most samples, and maximum observed density was 0.3 ind. m^{-3} for both *Lepeophtheirus salmonis* and

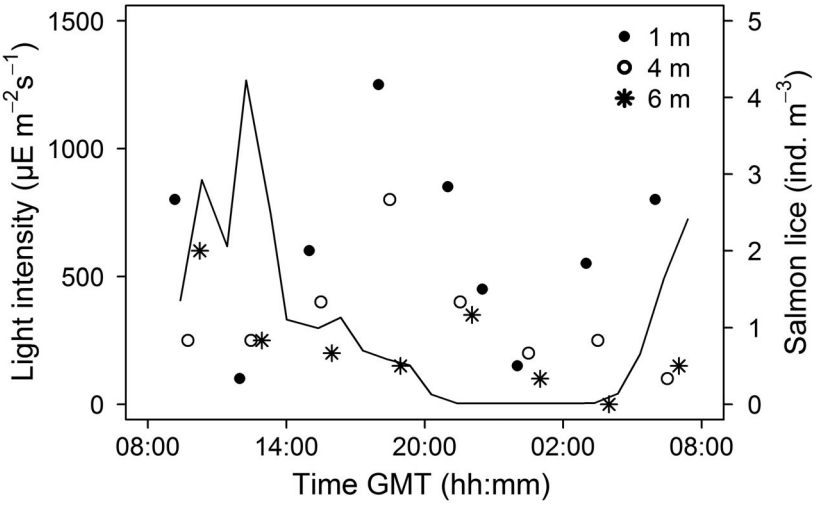

Fig. 4. Light intensity above the water column (line) and density of *Lepeophtheirus salmonis* at 3 different depths at the center of a salmon net cage during a 24 h measuring period from 6 to 7 May 2014

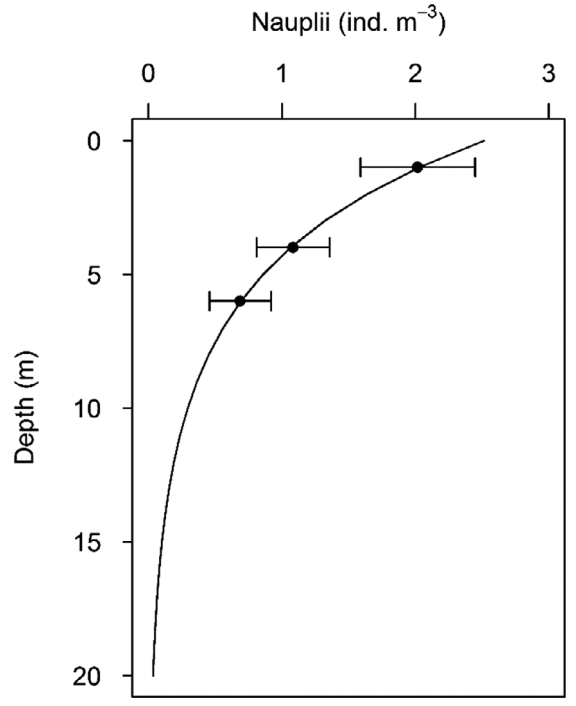

Fig. 5. Depth distribution of salmon lice nauplii in the fish cage (average ± SE, n = 9 at 1 m and n = 8 at 4 and 6 m depth). The line shows the fitted exponential decrease in nauplii abundance (Y) with depth (z) down to the bottom of the cage: $Y = 2.5e^{-0.215z}$ ($R^2 = 0.9994$, $p < 0.05$)

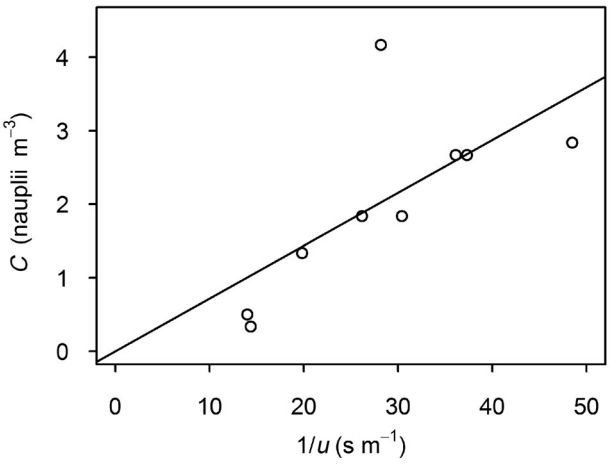

Fig. 6. *Lepeophtheirus salmonis* nauplii abundance C relative to the inverted current speed $1/u$ perpendicular to the cage at 1 m depth. The line denotes the linear relationship between current speed and nauplii abundance $C = 0.072 (1/u)$ ($R^2 = 0.87$, $p < 0.001$)

Caligus elongatus. In a comparable study at a farm in Ireland (Costelloe et al. 1996), the same maximum density of *L. salmonis* copepodids was observed. Similar abundances of *L. salmonis* copepodids are generally observed in open water (Costelloe et al. 1996, Morton et al. 2011, á Norði et al. 2015). In the Loch Torridon system, sea lice abundance has been intensively studied at 5 open-water stations over several years, and the long time average density of copepodids at the stations was in the range of 0.01 to 0.6 copepodids (cop.) m^{-3} (Penston et al. 2004, 2011). Nearshore and in river mouths, copepodids can be much more abundant, and densities >100 cop. m^{-3} have been reported (McKibben & Hay 2004, Penston et al. 2004).

While the present study was not able to provide information on the vertical distribution of copepodids due to their low abundance in the samples, our results show that nauplii abundance decreased with depth but no diel vertical distribution pattern was present. This finding for nauplii is comparable to previous observations (Costelloe et al. 1996, Gravil 1996). The dominance of nauplii at the fish farm is also similar to previous observations (Costelloe et al. 1996, Morton et al. 2011, Penston et al. 2011), and in the present study the nauplii were highly abundant downstream of the farm, contrasting against the few nauplii found upstream (Fig. 3). Thus, the farm clearly acted as a source of *L. salmonis* at the end of the grow-out period.

Sea lice prevalence on farmed fish generally increases towards the end of the farming cycle (Torrissen et al. 2013) and, accordingly, the nauplii abundance around fish farms has been found to increase with age of the farmed fish in the Broughton Archipelago (Morton et al. 2011).

In the effort to mitigate the salmon lice infection pressure on farmed and wild fish, the finding that nauplii are much more concentrated at the farm than the copepodids might be useful. Mitigating the infection pressure in farming systems by targeting nauplii at the source, before they are distributed over wide areas by the currents, could be accomplished more easily than preventing copepodids from reaching farmed fish.

The spatial distribution of *C. elongatus* nauplii was similar to that of *L. salmonis*, although the abundance was considerably higher (Fig. 3). Thus, the farm was also a source of *C. elongatus* nauplii in February. The *C. elongatus*/*L. salmonis* nauplii ratio was 2.7:1, while the ratio between gravid *C. elongatus* and *L. salmonis* on the farmed fish was only 1.7:1. This could indicate that, at the time of sampling, the *C. elongatus* nauplii production was higher than the *L. salmonis* production, despite the number of eggs per string being considerably smaller in *C. elongatus* (Hogans & Trudeau 1989, Pike & Wadsworth 1999).

However, sea lice on wild fish aggregating around the farm (Dempster et al. 2009) might have contributed to the nauplii production.

In the temporal study conducted in May, *C. elongatus* were absent from the plankton samples. This is related to the seasonal pattern in *C. elongatus* abundance in the Faroe Islands, as they are present in high numbers during winter and virtually absent during late spring and summer (á Norði et al. 2015).

Production of nauplii

The nauplii abundance inside a single fish cage varied considerably during the 24 h sampling period (Fig. 4). Greatest variation was observed at 1 m depth where the abundance was inversely related to the current speed at the same depth (Fig. 6). Costelloe et al. (1996) likewise observed a connection between nauplii density and current speed. In their study, current speeds below the measuring limit of 3 cm s^{-1} were continuously recorded for 2–3 h, at which time the nauplii abundance in the cages was between 20 and 60 ind. m^{-3}. At higher current speeds abundance ranged between 0 and 6 ind. m^{-3}.

Assuming the nauplii production to be constant over time and that the nauplii remain at the same depth inside the cage, the flux of nauplii per area equals the total production per area upstream the measuring point

$$P \cdot \Delta x = C \cdot u \quad (1)$$

where P is the nauplii production per volume in the cage, Δx is the distance upstream the measuring point inside the cage, C is the nauplii concentration and u is the current speed perpendicular to the cage. Thus, the slope in the linear model presented in Fig. 6 provides the total production at 1 m depth upstream of the measuring point ($P \cdot \Delta x = 0.072$ nauplii m^{-2} s^{-1}). From this production rate, together with the amount of females upstream of the measuring point and the depth distribution of nauplii production, the *in situ* nauplii production was estimated to 26–68 nauplii $female^{-1}$ d^{-1}.

A number of assumptions and estimates were used for the above calculation. It is assumed that the fish, and hence the sea lice production, is evenly distributed horizontally in the cage, and although the sea lice abundance was only measured down to 6 m depth, a depth distribution down to the bottom of the 20 m deep cage is assumed. According to the nauplii depth distribution, 17% of the total nauplii production occurred at 1 m depth. It is also assumed that the distance from the outmost point of nauplii release to the measuring point (12 m) is too short for their behavioural traits to influence their depth distribution.

The depth distribution of nauplii inside the fish cages is dependent on the swimming depth of the fish, which varies in response to environmental factors as well as feeding pattern and artificial light. Darkness during nighttime and continuous feeding at the surface during the day are both drivers that draw the fish towards the surface (Oppedal et al. 2001, 2011), and the increasing temperature towards the surface in May (á Norði et al. 2015) likewise suggests that the fish had a vertical distribution towards the surface (Oppedal et al. 2011). This corresponds well with the observed vertical nauplii distribution in Fig. 5. The nauplii depth distribution is a major factor when estimating the production. Thus, the swimming depth of the farmed fish should be included in future production estimates.

The current speed, which influences the outflow of nauplii, is only measured at 1 m depth outside the net cage in this study. However, other current speed measurements in the area (K. Simonsen unpubl. data) have shown the speed at 0–20 m depth generally to be within the range measured at 1 m depth in this study, and that vertical changes are small. The net cages impose a drag which causes a reduction in water flow through the cages. The exact reduction depends on various factors such as current speed, mesh size and biofouling. Also the presence of the fish influences the flow through the cages and increases mixing (Klebert et al. 2013). On the other hand, the current at the study site increased with distance to the shore (Fig. 2), and the current measurement was conducted closer to the shore than the sea lice sampling (Fig. 1). Therefore, the measured current speed is assumed to represent the flow in the cage.

Most of the production estimates presented in the literature are in the range of 20–30 nauplii $female^{-1}$ d^{-1}, as obtained from the combination of the number of eggs in egg strings, hatching rate and development time. (Johnson & Albright 1991, Stien et al. 2005, Kristoffersen et al. 2014, Serra-Llinares et al. 2014, Johnsen et al. 2016). This corresponds to the lower end (26 nauplii $female^{-1}$ d^{-1}) of the estimated production range in the present study.

In conclusion, this study has documented the farm as a source of salmon louse nauplii towards the end of the production cycle. Observations of the infective stage were scarce, and the study did not give insight into their origin. However, this study demonstrated a method to conduct *in situ* estimates of nauplii pro-

duction. Our estimates are in the same range, and therefore support, previous estimates of nauplii production that are based on laboratory trials, although the *in situ* estimate is associated with assumptions of unknown factors as discussed above. The production of nauplii only plays a partial role in the overall sea lice infection pressure, as during their planktonic stages, nauplii are subjected to various environmental conditions such as predation, risk of drifting to unsuitable environments, and failing to locate a suitable host. However, knowledge on the source and production rates is essential in the effort to mitigate infection pressure.

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LITERATURE CITED

á Norði G, Simonsen K, Danielsen E, Eliasen K and others (2015) Abundance and distribution of planktonic *Lepeophtheirus salmonis* and *Caligus elongatus* in a fish farming region in the Faroe Islands. Aquacult Environ Interact 7:15–27

Aaen SM, Helgesen KO, Bakke MJ, Kaur K, Horsberg TE (2015) Drug resistance in sea lice: a threat to salmonid aquaculture. Trends Parasitol 31:72–81

Aldrin M, Storvik B, Kristoffersen AB, Jansen PA (2013) Space-time modelling of the spread of salmon lice between and within Norwegian marine salmon farms. PLoS ONE 8:e64039

Asplin L, Johnsen IA, Sandvik AD, Albretsen J, Sundfjord V, Aure J, Boxaspen KK (2014) Dispersion of salmon lice in the Hardangerfjord. Mar Biol Res 10:216–225

Boxaspen K (2006) A review of the biology and genetics of sea lice. ICES J Mar Sci 63:1304–1316

Bricknell IR, Dalesman SJ, O'Shea B, Pert CC, Mordue Luntz AJ (2006) Effect of environmental salinity on sea lice *Lepeophtheirus salmonis* settlement success. Dis Aquat Org 71:201–212

Costello MJ (2006) Ecology of sea lice parasitic on farmed and wild fish. Trends Parasitol 22:475–483

Costelloe M (1998) Distribution of the larval stages of *Lepeophtheirus salmonis* in three bays on the west coast of Ireland. ICES J Mar Sci 55:181–187

Costelloe M, Costelloe J, Roche N (1996) Planktonic dispersion of larval salmon-lice, *Lepeophtheirus salmonis*, associated with cultured salmon, *Salmo salar*, in western Ireland. J Mar Biol Assoc UK 76:141–149

Dempster T, Uglem I, Sanchez-Jerez P, Fernandez-Jover D, Bayle-Sempere J, Nilsen R, Bjørn PA (2009) Coastal salmon farms attract large and persistent aggregations of wild fish: an ecosystem effect. Mar Ecol Prog Ser 385: 1–14

FAO (Food and Agriculture Organization of the United Nations) (2014) The state of world fisheries and aquaculture. FAO, Rome

Frenzl B, Stien LH, Cockerill D, Oppedal F and others (2014) Manipulation of farmed Atlantic salmon swimming behaviour through the adjustment of lighting and feeding regimes as a tool for salmon lice control. Aquaculture 424–425:183–188

Gaard E, á Norði G, Simonsen K (2011) Environmental effects on phytoplankton production in a Northeast Atlantic fjord, Faroe Islands. J Plankton Res 33:947–959

Genna RL, Mordue W, Pike AW, Mordue (Luntz) AJ (2005) Light intensity, salinity, and host velocity influence presettlement intensity and distribution on hosts by copepodids of sea lice, *Lepeophtheirus salmonis*. Can J Fish Aquat Sci 62:2675–2682

Gravil HR (1996) Studies on the biology and ecology of the free swimming larval stages of *Lepeophtheirus salmonis* (Kröyer, 1838) and *Caligus elongatus* Nordmann, 1832 (Copepoda: Caligidae). PhD thesis, University of Stirling

Heuch PA, Mo TA (2001) A model of salmon louse production in Norway: effects of increasing salmon production and public management measures. Dis Aquat Org 45: 145–152

Heuch PA, Parsons A, Boxaspen KK (1995) Diel vertical migration: a possible hostfinding mechanism in salmon louse (*Lepeophtheirus salmonis*) copepodids? Can J Fish Aquat Sci 52:681–689

Hevrøy EM, Boxaspen K, Oppedal F, Taranger GL, Holm JC (2003) The effect of artificial light treatment and depth on the infestation of the sea louse *Lepeophtheirus salmonis* on Atlantic salmon (*Salmo salar* L.) culture. Aquaculture 220:1–14

Hogans WE, Trudeau DJ (1989) Preliminary studies on the biology of sea lice, *Caligus elongatus*, *Caligus curtus* and *Lepeophtheirus salmonis* (Copepoda: Caligoida) parasitic on cage-cultured salmonids in the lower Bay of Fundy. Can Tech Rep Fish Aquat Sci 1715

Johnsen IA, Fiksen Ø, Sandvik AD, Asplin L (2014) Vertical salmon lice behaviour as a response to environmental conditions and its influence on regional dispersion in a fjord system. Aquacult Environ Interact 5:127–141

Johnsen IA, Asplin LC, Sandvik AD, Serra-Llinares RM (2016) Salmon lice dispersion in a northern Norwegian fjord system and the impact of vertical movements. Aquacult Environ Interact 8:99–116

Johnson SC, Albright LJ (1991) Development, growth, and survival of *Lepeophtheirus salmonis* (Copepoda: Caligidae) under laboratory conditions. J Mar Biol Assoc UK 71:425–436

Klebert P, Lader P, Gansel L, Oppedal F (2013) Hydrodynamic interactions on net panel and aquaculture fish cages: a review. Ocean Eng 58:260–274

Kristoffersen AB, Jimenez D, Viljugrein H, Grøntvedt R, Stien A, Jansen PA (2014) Large scale modelling of salmon lice (*Lepeophtheirus salmonis*) infection pressure based on lice monitoring data from Norwegian salmonid farms. Epidemics 9:31–39

Lien AM, Volent Z, Jensen Ø, Lader P, Sunde LM (2014) Shielding skirt for prevention of salmon lice (*Lepeophtheirus salmonis*) infestation on Atlantic salmon (*Salmo salar* L.) in cages—a scaled model experimental study on net and skirt deformation, total mooring load, and currents. Aquacult Eng 58:1–10

McKibben MA, Hay DW (2004) Distributions of planktonic sea lice larvae *Lepeophtheirus salmonis* in the inter-tidal zone in Loch Torridon, Western Scotland in relation to

salmon farm production cycles. Aquacult Res 35:742–750
Molinet C, Cáceres M, Gonzalez MT, Carvajal J and others (2011) Population dynamic of early stages of *Caligus rogercresseyi* in an embayment used for intensive salmon farms in Chilean inland seas. Aquaculture 312: 62–71
Molloy SD, Pietrak MR, Bouchard DA, Bricknell I (2011) Ingestion of *Lepeophtheirus salmonis* by the blue mussel *Mytilus edulis*. Aquaculture 311:61–64
Mordue (Luntz) AJ, Birkett MA (2009) A review of host finding behaviour in the parasitic sea louse, *Lepeophtheirus salmonis* (Caligidae: Copepoda). J Fish Dis 32:3–13
Morton A, Routledge R, McConnell A, Krkošek M (2011) Sea lice dispersion and salmon survival in relation to salmon farm activity in the Broughton Archipelago. ICES J Mar Sci 68:144–156
Oppedal F, Juell JE, Taranger GL, Hansen T (2001) Artificial light and season affects vertical distribution and swimming behaviour of post-smolt Atlantic salmon in sea cages. J Fish Biol 58:1570–1584
Oppedal F, Dempster T, Stien LH (2011) Environmental drivers of Atlantic salmon behaviour in sea-cages. Rev Aquacult 311:1–18
Orr C (2007) Estimated sea louse egg production from Marine Harvest Canada farmed Atlantic salmon in the Broughton Archipelago, British Columbia, 2003–2004. N Am J Fish Manage 27:187–197
Penston MJ, Davies IM (2009) An assessment of salmon farms and wild salmonids as sources of *Lepeophtheirus salmonis* (Krøyer) copepodids in the water column in Loch Torridon, Scotland. J Fish Dis 32:75–88
Penston MJ, McKibben MA, Hay DW, Gillibrand PA (2004) Observations on open-water densities of sea lice larvae in Loch Shieldaig, Western Scotland. Aquacult Res 35: 793–805
Penston MJ, Millar CP, Zuur A, Davies IM (2008) Spatial and temporal distribution of *Lepeophtheirus salmonis* (Krøyer) larvae in a sea loch containing Atlantic salmon, *Salmo salar* L., farms on the north-west coast of Scotland. J Fish Dis 31:361–371
Penston MJ, McBeath AJA, Millar CP (2011) Densities of planktonic *Lepeophtheirus salmonis* before and after an Atlantic salmon farm relocation. Aquacult Environ Interact 1:225–232
Pert CC, Fryer RJ, Cook P, Kilburn R and others (2014) Using sentinel cages to estimate infestation pressure on salmonids from sea lice in Loch Shieldaig, Scotland. Aquacult Environ Interact 5:49–59
Pike AW, Wadsworth SL (1999) Sealice on salmonids: their biology and control. Adv Parasitol 44:233–337
Salama NKG, Rabe B (2013) Developing models for investigating the environmental transmission of disease-causing agents within open-cage salmon aquaculture. Aquacult Environ Interact 4:91–115
Schram TA (2004) Practical identification of pelagic sea lice larvae. J Mar Biol Assoc UK 84:103–110
Serra-Llinares RM, Bjørn PA, Finstad B, Nilsen R, Harbitz A, Berg M, Asplin L (2014) Salmon lice infection on wild salmonids in marine protected areas: an evaluation of the Norwegian 'National Salmon Fjords'. Aquacult Environ Interact 5:1–16
Serra-Llinares RM, Bjørn PA, Finstad B, Nilsen R, Asplin L (2016) Nearby farms are a source of lice for wild salmonids: a reply to Jansen et al. (2016). Aquacult Environ Interact 8:351–356
Stien A, Bjørn PA, Heuch PA, Elston DA (2005) Population dynamics of salmon lice *Lepeophtheirus salmonis* on Atlantic salmon and sea trout. Mar Ecol Prog Ser 290: 263–275
Torrissen O, Jones S, Asche F, Guttormsen A and others (2013) Salmon lice—impact on wild salmonids and salmon aquaculture. J Fish Dis 36:171–194

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