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Gunnvør á Norði
Fiskaaling P/F - Aquaculture Research Station of the Faroes

Knud Simonsen
Fiskaaling P/F - Aquaculture Research Station of the Faroes

Agnes Mols-Mortensen
TARI - Faroe Seaweed and Fiskaaling - Aquaculture Research Station of the Faroes

Debes Hammershaimb Christiansen
Faroese Food and Veterinary Authority

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Abundance and distribution of planktonic *Lepeophtheirus salmonis* and *Caligus elongatus* in a fish farming region in the Faroe Islands

G. á Norði[1,]*, K. Simonsen[1], E. Danielsen[1], K. Eliasen[1], A. Mols-Mortensen[1], D. H. Christiansen[2], P. Steingrund[3], M. Galbraith[4], Ø. Patursson[1]

[1]Fiskaaling - Aquaculture Research Station of the Faroes, við Áir, 430 Hvalvík, Faroe Islands
[2]Faroese Food and Veterinary Authority, V. U. Hammershaimbsgøta 11, 100 Tórshavn, Faroe Islands
[3]Faroe Marine Research Institute, Nóatún 1, 100 Tórshavn, Faroe Islands
[4]Fisheries and Oceans Canada, Institute of Ocean Sciences, 9860 West Saanich Road, Sidney, British Columbia W8L 4B2, Canada

ABSTRACT: The abundance of planktonic sea lice in the surface waters of the strait of Sundalagið, Faroe Islands was investigated from November 2013 to June 2014. The strait is 38 km long and hosts 6 salmon farms with coordinated farming cycles. The spatial distribution of planktonic sea lice for the entire strait was examined in 2 surveys with different wind and hydrographic conditions. Temporal changes were investigated every 2–3 wk at 3 set stations throughout the study. The spatial distribution of *Lepeophtheirus salmonis* copepodids was clearly influenced by the actual wind direction, as the copepodids were found where winds pushed surface waters towards the shore. The same spatial pattern was not found for *Caligus elongatus* copepodids. This might be related to a different vertical migration pattern. The abundance of *C. elongatus* was seasonal. It was the dominant planktonic sea louse during winter, with a mean abundance of 0.34 ± 0.13 ind. m^{-3}, and was virtually absent during summer. *Lepeophtheirus salmonis* was present throughout the study, except during the last survey when the coordinated farming sites lay fallow. During winter when the warmest seawater was deep in the water column, *L. salmonis* copepodids were present in 47% of the samples and nauplii were only observed in 9%. In samples where the highest seawater temperature was at the surface, nauplii prevalence attained a high value of 53%, while copepodid prevalence increased to 60%. These results indicate that nauplii might actively seek the highest possible seawater temperature.

KEY WORDS: *Lepeophtheirus salmonis* · *Caligus elongatus* · Sea lice · Infectious copepodid · Nauplii · Aquaculture

INTRODUCTION

Sea lice are ubiquitously associated with salmon farms, and have been rated as the most damaging parasites in the salmon farming industry (Costello 2006). In Faroese fish farming areas, the temperature (6–12°C) and salinity (>30) are highly suitable for Atlantic salmon *Salmo salar* L., 1758 farming, as well as for production of sea lice (Johnson & Albright 1991). Like elsewhere in the Atlantic Ocean (Boxaspen 2006), the 2 most abundant sea lice species on salmon farmed in Faroese waters are the salmonid specialist *Lepeophtheirus salmonis* (Krøyer, 1837), and the teleost generalist *Caligus elongatus* (Nordmann, 1832), which has been found on >80 fish species (Kabata 1979).

Both species have 2 planktonic nauplii stages prior to the infective copepodid stage. The duration of the nauplii stages is temperature dependent, with shorter development time at higher temperatures

*Corresponding author: gunnvor@fiskaaling.fo

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(Pike et al. 1993, Stien et al. 2005). The limited endogenous energy supply defines the period in which the infective copepodid has to find a suitable host, where the ectoparasitic life cycle stage is initiated (Piasecki & MacKinnon 1995, Hamre et al. 2013).

Lepeophtheirus salmonis has been investigated to a larger extent than other sea lice species (Boxaspen 2006). The planktonic stages migrate vertically in response to environmental stimuli — e.g. swimming towards light (Heuch et al. 1995) and avoidance of freshwater (Bricknell et al. 2006). To our knowledge, sensing of temperature has not been observed in laboratory experiments, but model simulations have shown that it would be beneficial for nauplii to seek the highest possible temperature vertically, as this would reduce the duration of nauplii stages by up to 1 d, hence decreasing the risk of mortality (Johnsen et al. 2014).

Copepodids respond to chemical and mechanical stimuli with burst swimming, which plays a role in host finding (Gravil 1996, Pike & Wadsworth 1999, Mordue & Brikett 2009). However, when transported over distances, sea lice are thought to drift passively with the currents (Boxaspen 2006), and can easily be transported several kilometres away from their origin (Salama & Rabe 2013, Asplin et al. 2014).

In coastal environments, the planktonic stages of *L. salmonis* are most abundant in the upper few meters of the water column (Heuch et al. 1995, Hevrøy et al. 2003, McKibben & Hay 2004, Penston et al. 2004). Copepodids tend to aggregate in shallow estuarine areas, which are ideal locations for intercepting migratory salmonids (Pike & Wadsworth 1999, McKibben & Hay 2004, Penston et al. 2004, Costello 2006). In fact, the highest densities of copepodids have been found by wading and towing plankton nets along the shore (McKibben & Hay 2004, Penston et al. 2004). Copepodids are the main infective life cycle stage of the species, but infection by preadults and adults have also been observed in the field (Pert et al. 2014).

Caligus elongatus adults readily transfer between hosts and species (Øines et al. 2006) and have been found on several species which are commercially fished in Faroese waters, including cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), saithe (*Pollachius virens*), mackerel (*Scomber scombrus*), and herring (*Clupea harengus*) (Neilson et al. 1987, MacKenzie & Morrison 1989, Øines et al. 2006, Heuch et al. 2007). All of these fish species inhabit the coastal zone to various degrees, and aggregate around fish farms (Dempster et al. 2009).

Infestation of farmed fish by *C. elongatus* is often seasonal. In Scotland, the epidemiology of *C. elongatus* on farmed fish shows increased infection from June to late September (Revie et al. 2002, McKenzie et al. 2004). In the central and northern parts of Norway, high *C. elongatus* abundance on farmed fish frequently occurs in autumn (Øines et al. 2006). Infections have been assumed to be connected to passing schools of pollock, saithe or herring. In British Columbia, epizootics of *C. clemensi* infestations on wild and farmed salmonids have occurred as migrating Pacific herring enter the area during winter (Morton et al. 2008, Beamish et al. 2009).

A study of wild fish on the coast of Norway showed that *C. elongatus* was present on 27 of 52 species caught, several of which had higher infestation during autumn (Heuch et al. 2007). This observation demonstrates the difficulty in determining the causal mechanism or species in the seasonal infestation pattern that is often observed on farmed fish, as correlations between species are likely to be due to derived rather than causal reasons.

The present study investigated the seasonal and spatial abundance of planktonic *L. salmonis* and *C. elongatus* in the coordinated fish farming region of Sundalagið, Faroe Islands. The study also included simultaneous investigation of winds and hydrography, and differentiated between sea louse species both in the copepodid and nauplii stages. This approach enabled investigations on the seasonal and farming dependent abundance of the 2 species, as well as the influence of hydrography on distribution. This study provides the first information on the abundance and distribution of planktonic sea lice in Faroese waters.

MATERIALS AND METHODS

Study area

The study was conducted in Sundalagið, which is a ~38 km long strait between the 2 largest islands in the Faroes. Sundalagið consists of 2 main basins separated by a narrow (150 m) and shallow (4 m) sill (Fig. 1). The northern basin is narrow (~1 km), 11 km long, is separated from the open ocean by a 10 m deep sill, and has a maximum bottom depth of 60 m. The southern basin is wider and deeper than the northern basin and has 3 adjacent fjords. Its maximum depth is 80 m and the sill that restricts the strait southward into a deeper and more energetic strait is 40 m deep (Fig. 1).

In the southern basin, the tidal influence is small as this area is part of a semi-amphidromy in the otherwise dominating semi-diurnal tides (Simonsen & Nic-

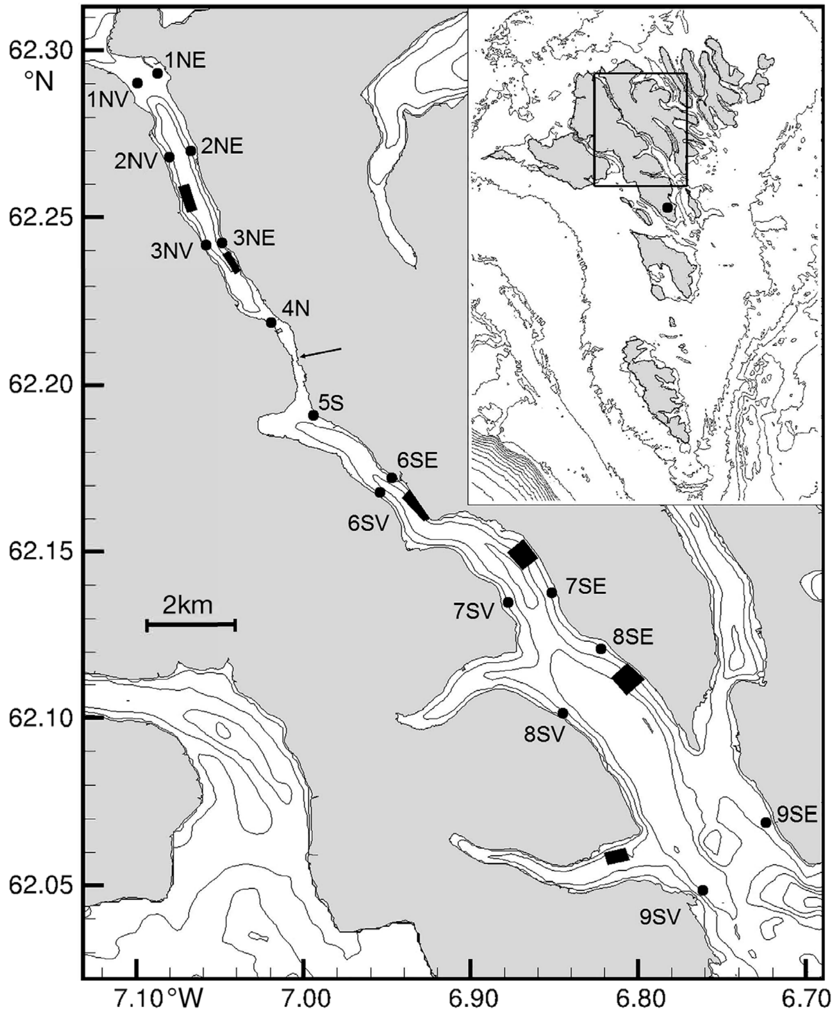

Fig. 1. Sampling stations (●) and salmon farming areas (black blocks). The arrow points out the narrow and shallow sill that divides Sundalagið into 2 main basins. N, S, E, V: stations located in the northern and southern basins, and in the eastern and western shores, respectively; isobaths for every 20 m depth; inset: location of the study area in relation to Faroe Islands (with 50 m isobaths); (● in inset): the weather station Glyvursnes

lasen 2011), while the tidal range may exceed 2 m in the northern basin. This creates quite strong currents above the shallow sill between the 2 basins; otherwise, circulation is generally wind and freshwater driven. Seawater from the Faroe shelf enters Sundalagið at both ends of the strait. The relatively saline water mainly enters the strait at depth in the water column, and is overlaid by less saline water brought in by freshwater runoff particularly in the northern basin. This leads to weak and variable stratification of the surface waters.

Due to the highly variable weather conditions, with wind and precipitation changing within short time scales, hydrodynamics driven by wind and freshwater are also highly changeable (Gaard et al. 2011). However, circulation in the northern basin is more affected by tides than that in the southern basin.

In the period 2010 to 2014, there were 6 active fish farms in Sundalagið and adjacent fjords (Fig. 1), with coordinated farming and production cycles of 18 mo, followed by a fallowing period of at least 2 mo as required by legislation. However, in order to organize the coordination between the farms, the fallow period was substantially longer at most farms.

At the onset of the study, the farms were at the end of the grow-out period. In the southern basin, harvesting commenced in October 2013 and was finalized by April 2014. From this date, there were no farmed fish in the southern basin. In the northern basin, harvesting commenced in March 2014, and was finalized on June 10, 2014; consequently, there were no farmed fish in Sundalagið during the last survey. The number of adult female *Lepeophtheirus salmonis* during the study was constantly <2 per fish, which is the legislated maximum allowable abundance.

Sampling

The sampling period was from November 18, 2013 to June 23, 2014. Two sampling protocols were used — one to focus on temporal changes and the other to address spatial changes.

During winter, the relatively high seawater temperature (6°C) is suitable for sea lice production (Stien et al. 2005); combined with the absence of primary production (Gaard et al. 2011), this made it practical to sample as many as 16 stations (Fig. 1) and investigate the entire sample content with a stereomicroscope within 1 wk of each survey. The comprehensive sampling effort made it possible to obtain an overview of the spatial distribution of planktonic sea lice in the investigated area. The 16 stations were located along both sides of the strait and 2 surveys were conducted.

Temporal changes in the abundance of planktonic sea lice were investigated at 3 stations every 2 to 3 wk. Two of the time series stations (Stns 3NE and 4N) were in the northern basin where 2 fish farms were located (Fig. 1). Stn 3NE was located ~600 m northwest of a fish farm, while Stn 4N was 2.3 km southeast of the same farm (Fig. 1). Surface currents at the farm were predominantly in a NW direction (Ø. Patursson unpubl. data). The third time series station (Stn 5S) was located in the southern basin. The distance to the nearest fish farm was ~5 km. At that particular farm, the last fish were harvested in late February 2014.

Samples were taken using a 150 µm mesh size plankton net, with a mouth diameter of 50 cm and a length of 1.5 m. To keep the net at a constant depth and the mouth perpendicular to the surface, floats and weights were mounted on it. The uppermost part of the mouth was at ~0.25 m below the surface. The plankton net was towed from a 7.92 m boat. Tows started as close to the shore as possible (distance to shore = 10 to 30 m), and were taken seawards for 200 ± 21 m, with a constant speed of 1.5 knots. At Stn 4N which is in the narrow passage in the sound (Fig. 1), tows were taken from shore to shore across the sound (~240 m). The towing distance was monitored using a GPS (Garmin®). The towing distance and mouth area of the plankton net were used to calculate the volume of filtered seawater. In May, the volume of filtered seawater was affected by some clogging of the net due to the abundance of phytoplankton in the seawater. For the rest of the year, the samples showed no signs of clogging.

Vertical profiles of temperature and salinity were recorded using a CTD (Sea-Bird Electronics, SBE 25plus) at the offshore end of each tow, except for Stn 4N, where the profile was taken at the midpoint of the transect. The instrument stored 8 scans s^{-1}, and was lowered by hand at a speed of ~0.75 m s^{-1}. The data were low-pass filtered and obvious spikes were removed before averaging data into 1 m bins.

Meteorological observations were obtained at a weather station in Glyvursnes (Fig. 1). This weather station is representative of general wind directions in the Faroe Islands, as the influence of local topography is limited. The station is operated by Landsverk (the local road and harbour authorities) and the data was acquired from their online service (www.landsverk.fo). Records of 10 min mean values of wind speed and direction were used.

Identification

Samples were preserved in ethanol (99.9%) and counted within 1 wk of sampling. The entire content was analyzed using a stereomicroscope, and the nauplii and copepodids were identified by their morphometrics and pigmentation pattern and colour (Schram 2004; *L. salmonis* have black and brown pigmens while the pigments in *C. elongatus* are red. Reference was also made to nauplii and copepodids from *L. salmonis* and *Caligus elongatus* egg strings hatched in the laboratory (Danielsen 2013) to facilitate identification of the 2 species in mixed field samples. Except for a few specimens (<1%), all of the sea lice nauplii were identified to species level. The nauplii that were not identified to species had washed out pigmentation.

Real-time PCR

For specific identification of *L. salmonis* and *C. elongatus*, a duplex real-time PCR assay was used. DNA was extracted from individual sea lice using the DNeasy mini kit or QIAsymphony DNA kit (Qiagen) following manufacturer recommendations. Duplex real-time PCR was performed using the QuantiTect Probe™ kit (Qiagen), including *L. salmonis* and *C. elongatus* primers (1 µM) and TaqMan® MGB probes (200 nM) as designed by McBeath et al. (2006). Amplification was performed on an ABI 7500 FAST Sequence Detection System (Applied Biosystems), with the following cycling profile: activation of the HotStart Taq polymerase at 95°C for 15 min, followed by 30 cycles of 94°C for 15 s and 60°C for 1 min.

In order to evaluate the possible presence of sea lice other than *L. salmonis* and *C. elongatus* in the plankton, the real-time PCR assay was run on nauplii from 2 of the plankton samples. At the time the nauplii were selected for real-time PCR, no pigmentation was visible; thus, the identity of the analyzed nauplii was unknown. In addition, chalimus stages that were randomly sampled from farmed Atlantic salmon in the Faroes have been analyzed routinely using real-time PCR assay from 2010 to 2014.

Pearson's Chi square tests with Yates' Correction for Continuity (Fowler et al. 1998) were performed, with the null hypothesis that the identification of nauplii by microscopy was consistent with the real-time PCR assay. All statistics were performed with the statistical software package R (www.r-project.org).

Sea lice on farmed fish

Data on *C. elongatus* abundance on farmed fish was supplied by Marine Harvest Faroes, which operated 2 of the 6 fish farms in Sundalagið. The data was

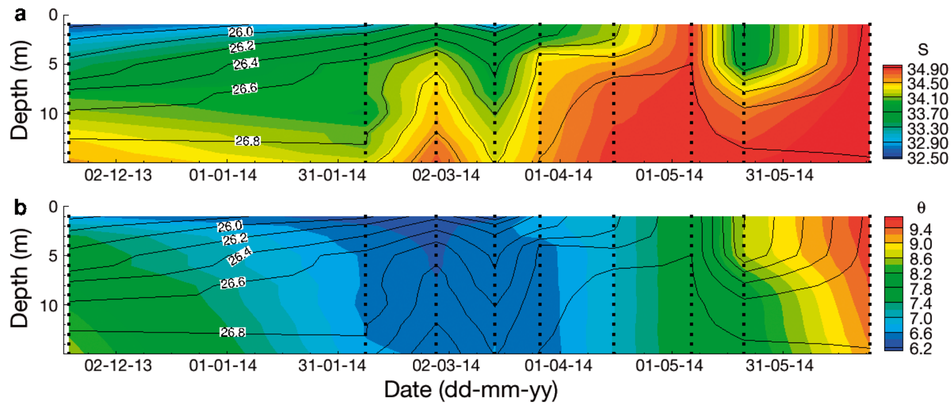

Fig. 2. (a) Salinity, (b) potential temperature (θ) and potential density (σ_θ; black contours in both plots) in the upper 15 m at station 3NE from November 18, 2013 to June 23, 2014. Vertical stippled lines denote sampling dates

obtained from the legislated sea lice monitoring programme during the latest 2 production cycles at the farms. Sea lice were counted on 10 fish in each of 4 cages fortnightly, and were grouped into gravids or adults.

RESULTS

Hydrography and wind

The water column was stratified on most sampling dates. During winter, the influence of freshwater runoff produced gradients in salinity and density near the surface, while a more homogenous surface layer down to 10 m depth was observed in late spring (Fig. 2).

Surface waters had the lowest salinity of 32.5 in November, and continued to be relatively fresh until late spring (Fig. 2a). During winter and early spring, the low salinity surface water was colder than the deeper water masses. The minimum sea surface temperature of 6.1°C was observed in late February (Fig. 2b). In late March, the surface layer had become slightly warmer than the underlying water, and the general heating continued throughout the rest of the study, reaching the maximum temperature of 9.7°C in the last record. This indicates that the highest seawater temperature was at the surface from late March and onwards, as opposed to the winter conditions, when the warmest water was located deeper in the water column (Fig. 2b). Temperature and salinity at 1 m depth did not differ much among the 3 time series stations (3NE, 4N and 5S; data not shown).

The influence of winds on the upper water masses was evident when comparing the regional samplings in November 2013 and February 2014. This was most pronounced in the southern basin. In November, there was relatively steady weather with northwest and westerly winds, with mean velocities between 4 and 13 m s^{-1} in the 12 h prior to the field sampling (Fig. 3). Stratification was deeper and salinity was lower on the east side of the sound compared to the west side in the southern basin (Fig. 4a,b). In the 12 h prior to the field study in February, winds came from the opposite direction, with velocities between 2 and 11 m s^{-1} (Fig. 3b). Under these circumstances, the southern basin showed deeper stratification and lower salinities on the west side of the sound (Fig. 4c,d). Except for the northernmost station, where a hydropower outlet influenced the salinity particularly at Stn 1NE (Fig. 4), the northern basin showed no pronounced difference in salinity between the east and west side of the sound on either of the sampling dates.

In order to investigate the representativeness of the wind conditions prior to the study, 1 yr wind records (July 1, 2013 to June 30, 2014) were analyzed. Winds from the same directions as those occurring for at least 12 h prior to the 2 regional samplings were recorded in 11 and 28 % of the time for the November and February samplings, respectively. The higher occurrence of the same conditions as those in February is due to the wider span in the wind direction. In the 12 h prior to the samplings, the wind speed did not exceed 13 m s^{-1} (Fig. 3), which was the situation in 87 % of the time in the considered year.

Spatial distribution

Lepeophtheirus salmonis copepodids were found in 7 of the 16 stations in November. The stations were evenly distributed across the northern and southern parts of the sound. However, 5 of the stations where *L. salmonis* was found were located on the east side of the sound (Table 1). The average density of *L.*

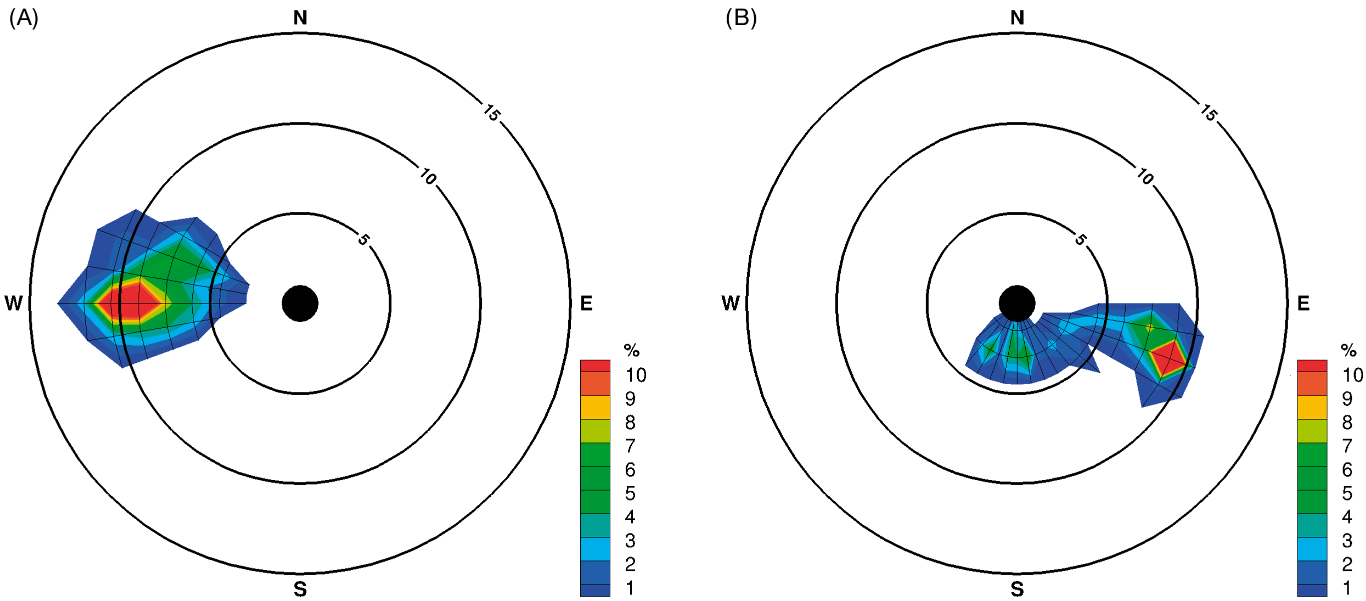

Fig. 3. Frequency plot of wind direction and speed (in 10° and 1.5 m s^{-1} intervals, respectively) during the 12 h period prior to the spatial surveys in (A) November 2013 and (B) February 2014

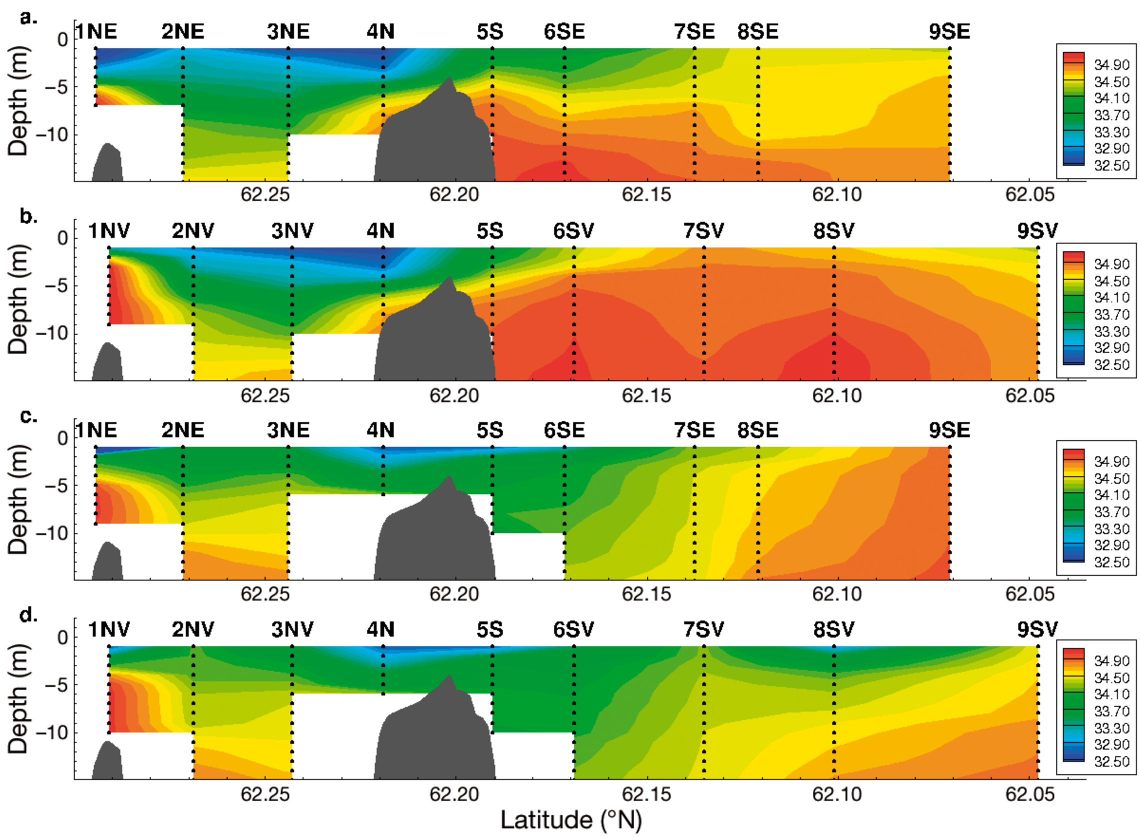

Fig. 4. Salinity in the upper 15 m of the water column during the spatial surveys in (a,b) November 2013 and (c,d) February 2014. Grey area: bottom depth at the 2 shallow sills separating the northern basin from the open ocean (left grey area), and the southern from the northern basin (middle grey area). Stations are as in Fig. 1

Table 1. *Lepeophtheirus salmonis* and *Caligus elongatus*. Densities of nauplii and copepodids in the top meter of the water column on November 18, 2013 and February 26, 2014. N, S, E, W: stations located in the northern and southern basins, and in the eastern and western shores, respectively

Station	*L. salmonis* nauplii (ind. m^{-3})		*L. salmonis* copepodids (ind. m^{-3})		*C. elongatus* nauplii (ind. m^{-3})		*C. elongatus* copepodids (ind. m^{-3})	
	Nov.	Feb.	Nov.	Feb.	Nov.	Feb.	Nov.	Feb.
1NW	0	0	0	0	0.02	0	0.02	0.10
1NE	0	0	0	0	0.03	0	0.05	0
2NW	0	0	0.02	0	0	0.05	0.05	0.03
2NE	0	0	0	0.03	0	0	0.08	0.28
3NW	0	0	0	0	0.05	0	0.08	0.05
3NE	0	0	0.06	0.02	0	0	0.09	0.10
4N	0	0	0.06	0.06	0.02	0.02	0.21	0.13
5S	0	0	0.03	0	0.24	0	0.3	0
6SW	0	0	0	0.10	0.03	0	0.11	0.03
6SE	0	0	0.03	0.21	0	0	0.15	0
7SW	0	0	0	0.13	0.08	0	0.05	0.03
7SE	0	0	0	0	0	0	0.20	0.05
8SW	0	0	0	0.17	0	0	0.02	0.02
8SE	0	0	0.05	0	0	0.03	0.02	0
9SW	0	0	0	0.04	0.02	0	0.34	0.04
9SE	0	0	0.03	0	0	0	0.13	0.03

salmonis copepodids was 0.02 cop. m^{-3} both in the northern and southern basins.

There were only minor changes in the *L. salmonis* abundance in the northern basin between the November and February sampling periods, but the average abundance had increased to 0.07 cop. m^{-3} in February in the southern basin. The copepodids were mostly found on the west side of the sound although the fish farms were located on the east side (Table 1).

The pooled number of *L. salmonis* in the plankton samples from the east and west sides of Sundalagið differed significantly between the 2 surveys with different hydrodynamic conditions ($\chi^2 = 4.77$, df = 1, $p < 0.05$). Such statistical difference was not observed in *Caligus elongatus* ($\chi^2 = 0.009$, df = 1, p = 0.92).

Caligus elongatus were highly abundant in November, with copepodids being present in all stations (Table 1). The average density of *C. elongatus* copepodids was 0.08 cop. m^{-3} in the northern basin, and almost twice as high in the southern basin. It was also in the southern basin, at Stn 9SW, where the highest density (0.34 cop. m^{-3}) was observed. The average abundance showed a small increase to 0.10 cop. m^{-3} in February in the northern basin, but decreased from 0.15 cop. m^{-3} in November to 0.02 cop. m^{-3} in February in the southern basin. There were substantially fewer nauplii than copepodids (ratio 1:6.5) during the 2 regional samplings and all of these were *C. elongatus* (Table 1).

Temporal changes

Throughout the study, the abundance of *L. salmonis* was below 0.2 ind. m^{-3} at Stns 4N and 5S. Temporal changes were not that evident at Stn 5S, but abundance was higher during spring than in winter at Stn 4N (Fig. 5). At Stn 3NE, which was ~600 m downstream of a fish farm, *L. salmonis* was much more abundant. Clear seasonal trends were observed at this station, with low numbers until early March, followed by a peak in abundance of 3.2 ind. m^{-3} in late March, and a quick subsequent decline (Fig. 5). No planktonic sea lice were observed at Stn 3NE from mid-May to the end of the study. At the other 2 stations, sea lice were also scarce towards the end of the study. By the last field trip, all the farms in Sundalagið lay fallow and no planktonic stages of *L. salmonis* were found.

From the onset of the investigation to late February, *C. elongatus* was the dominant sea louse species at all stations (Fig. 5). The highest density was observed in mid-February at Stn 5S (0.96 ind. m^{-3}). During March, the species composition started to change, and only one planktonic *C. elongatus* was observed in the samples from April to the end of the study (Fig. 5).

During winter, when *C. elongatus* was the most abundant sea louse species, copepodids dominated the planktonic stages; the shift towards higher abundance of *L. salmonis* in the succeeding months was largely due to nauplius stages (Fig. 6). The dominance of nauplii was especially pronounced at

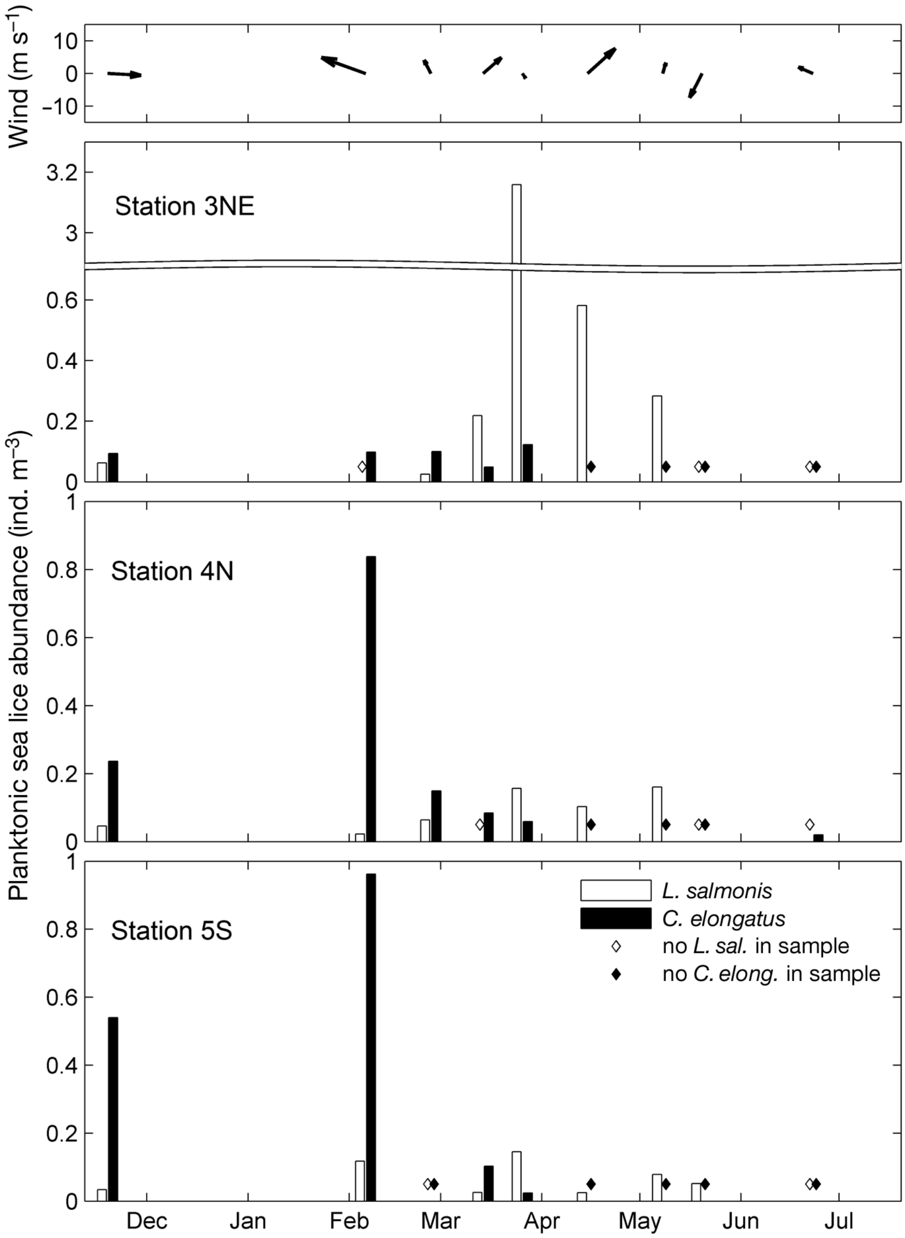

Fig. 5. *Lepeophtheirus salmonis* (white) and *Caligus elongatus* (black). Time series of abundance (nauplii and copepodids) in the top meter of the water column at stations 3NE, 4N and 5S. Bars: densities, diamonds: samples with no sea lice. Arrows in uppermost panel: wind direction and speed averaged over 12 h prior to the field investigations

Stn 3NE, where the nauplii to copepodid ratio ranged between 4 and 8 in March and April. At Stn 4N, the ratio ranged between 0.14 and 4 in the same period.

The abundance of gravid *C. elongatus* on fish farmed in Sundalagið changed with season, with low abundances during the summer months (Fig. 7). In the southern basin, the initial increase in abundance typically occurred in September and peaked from November to January. In the northern basin, abundance increased later, with peak abundance occurring in February (Fig. 7).

Reliability in identification

Lepeophtheirus salmonis and *C. elongatus* are the most abundant sea lice on farmed salmon in the Faroe Islands. Of a total of 520 chalimi stage individuals sampled randomly from farmed Atlantic salmon, 147 and 366 were identified as *L. salmonis* and *C. elongatus*, respectively, using duplex real-time PCR assay. Thus, only 7 sea lice were unidentified.

The real-time PCR results showed that *C. elongatus* and *L. salmonis* contributed largely to the plank-

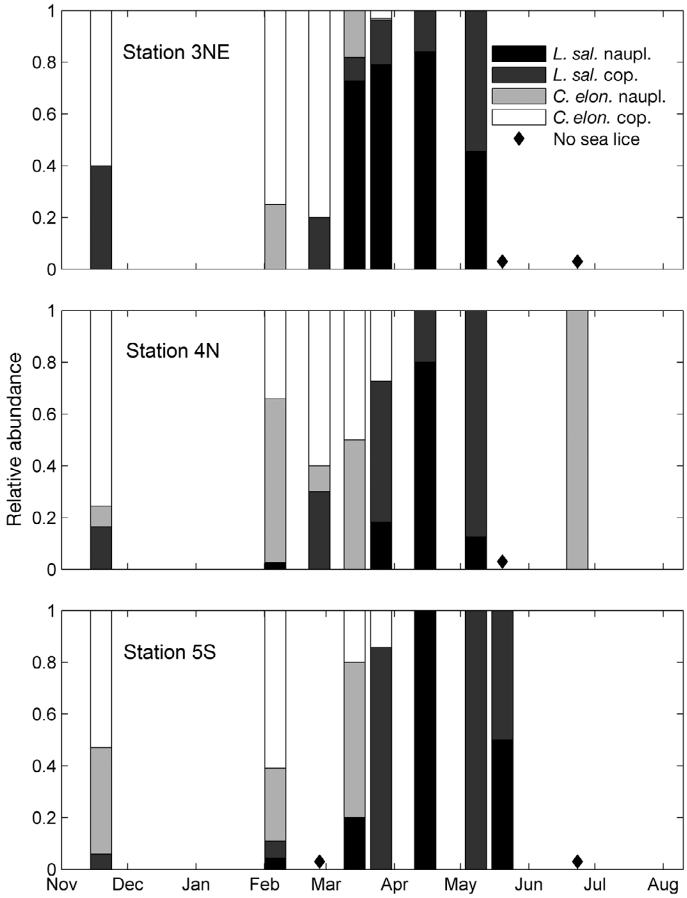

Fig. 6. *Lepeophtheirus salmonis* and *Caligus elongatus*. Relative abundance of nauplii and copepodids in the top meter of the water column from November 2013 to June 2014 at the 3 time series stations

ton samples, as all the 35 nauplii identified by the method were either of the 2 species. Further, the results confirmed the high reliability of the identification of nauplii through their pigmentation.

In a plankton sample containing 21 nauplii identified as *L. salmonis* through their pigmentation, real-time PCR was run on 10 nauplii and the identity was confirmed. In a second sample, with dominance of *C. elongatus* (n = 49), a few *L. salmonis* (n = 3) and a high number of unidentified nauplii (n = 5), the assay was run on 23 of the nauplii. The assay identified one nauplius as *L. salmonis* and the remaining 22 as *C. elongatus*. Thus, the frequency of *C. elongatus* was high using both real-time PCR and stereomicroscopic investigation of the total sample. Approximately 96 % of the nauplii tested by real-time PCR were *C. elongatus*, while their occurrence in the total sample was 85 to 95 % depending on the identity of nauplii with faded pigmentation.

DISCUSSION

This study provides the first insight into the spatial and temporal distribution of planktonic sea lice in the Faroe Islands. The density of planktonic sea lice was within the range found in other regions (Costelloe et al. 1998, Penston et al. 2004, 2008, 2011, Penston & Davies 2009, Molinet et al. 2011, Morton et al. 2011). However, the reported densities are highly variable depending largely on distance to shore and to fish farms. *Lepeophtheirus salmonis* nauplii are most commonly found near fish farms, with the nauplii to copepodid ratio decreasing with distance to farms (Costelloe et al. 1996, Penston et al. 2004, 2008, Morton et al. 2011). This was also the case in the present study (Fig. 6).

Spatial distribution

The 2 spatial surveys showed pronounced influence of winds on the hydrography of the southern basin in Sundalagið. In the 12 h prior to the sampling in November, winds came from the west (Fig. 3), and the less saline surface water was pressed towards the eastern shore (Fig. 4). At that time, *L. salmonis* were only found in the eastern shore (Table 1). In February, winds pushed the surface waters westwards, and *L. salmonis* were again found in the less saline water along the western shore.

The local weather changes quite rapidly (Gaard et al. 2011), and the representativeness of the physical conditions during the 2 spatial surveys as general situations in the local area might be limited. Nevertheless, this study provides a direct observation of the influence of winds on the hydrography and distribution of planktonic *L. salmonis*; the reversed distribution of sea lice in Sundalagið during the 2 different dates could be explained by the wind and hydrographic conditions at the time of the field studies. This highlights the importance of applying hydrodynamic models that include wind patterns when modelling infection pressure of *L. salmonis*, as also emphasized by Salama & Rabe (2013) and Johnsen et al. (2014). Such models predict the distribution of planktonic sea lice to be patchy and that they tend to accumulate in areas close to the shore (Amundrud & Murray 2009, Salama & Rabe 2013, Asplin et al. 2014). This is also the general observation in field studies of *L. salmonis* copepodids (McKibben & Hay 2004, Penston et al. 2004, Penston & Davies 2009).

The spatial distribution of *Caligus elongatus* copepodids did not reflect the hydrographic conditions in

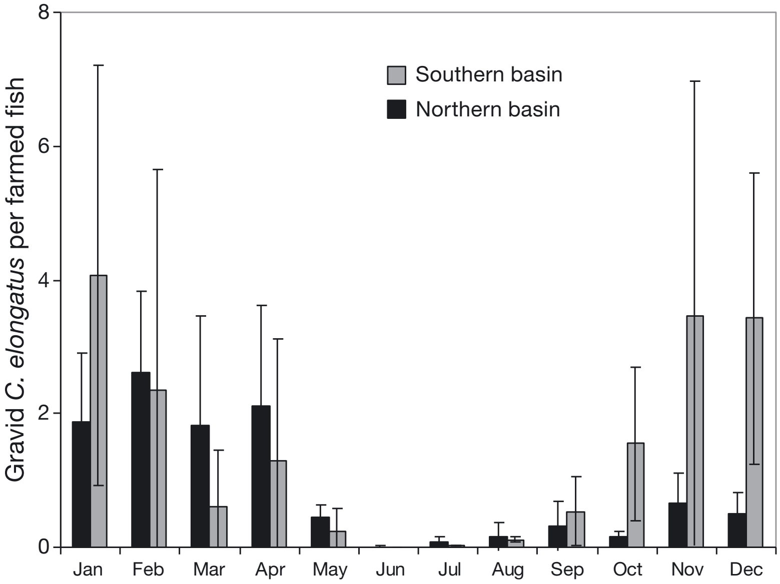

Fig. 7. Monthly averaged abundance of gravid *Caligus elongatus* during 2 farming cycles (2010–2014) at a salmon farm in the southern basin in Sundalagið (grey bars) and a farm in the northern basin (black bars). Error bars: SE between years

the upper water masses as clearly as the spatial distribution of *L. salmonis* (Table 1). This might be due to different vertical migration strategies between the 2 species. *Lepeophtheirus salmonis* copepodids are most abundant in the top 4 m of the water column (Hevrøy et al. 2003, Costello 2006), and although they show diel vertical migration, they only migrate small distances and still swim high in the water column at night (Heuch et al. 1995). Thus, they are continuously dispersed with surface currents that are influenced by winds.

Knowledge on the vertical distribution and migration of *C. elongatus* copepodids is scarce, as most studies focus on *L. salmonis*. However, given its wide range of hosts, it may not necessarily be beneficial for *C. elongatus* copepodids to constantly seek the upper few meters of the water column.

A study on *C. elongatus* infesting haddock suggests that larvae are distributed in mid water, intercepting haddock that swim through this zone (Costello 1993). Moreover, copepodids of a related species (*Caligus rogercresseyi*) have been found to be common below the pycnocline, despite being more abundant in surface waters, especially during the day (Molinet et al. 2011). If the vertical migration of *C. elongatus* exceeds the depth of stratification, their abundance at the top of the water column might be less affected by the actual wind situation compared to *L. salmonis*, given the shorter period of drifting with the surface currents.

Temporal changes

Other studies have found correlations between the abundance of gravid *L. salmonis* on farmed fish and copepodid abundance (Penston & Davies 2009, Pert et al. 2014). In this study, planktonic *L. salmonis* were completely absent in the samples when the region lay fallow, and they were scarce during earlier field trips when the number of farmed hosts was low (Fig. 5).

At the last 2 field surveys, the wind direction might have had an influence on the absence of sea lice at Stn 3NE, as the wind may have directed the water masses from the closest fish farm southwards in late May and away from the shore in June (Fig. 5). On the other hand, the 2 spatial surveys showed small influence from winds in the northern basin, where tidal currents are stronger than in the southern basin (Fig. 4). Stn 4N was sampled across the sound covering both shores, and should be less affected by the actual wind situation. *L. salmonis* was absent in the last 2 time series samples at Stn 4N.

The peak in *L. salmonis* abundance (3.2 ind. m^{-3}, of which 80% were nauplii) was observed in late March at Stn 3NE (Figs. 5 & 6). The field sampling took place during a bath treatment for sea lice at the nearest fish farm. This was part of the annual national coordinated delousing, which took place from mid-March to mid-April. Penston et al. (2004) observed pulses of larvae in Loch Shieldaig and speculated that sea lice treatments could trigger release of nauplii from egg strings of farmed lice. They further stated that the treatment just pre-empted a natural release of larvae. In Sundalagið, the numbers of planktonic *L. salmonis* had started to increase prior to the delousing activity, and remained elevated until mid-May (Fig. 5). In addition, the nature of egg production by females implies that it is highly unlikely for females to respond in the limited period of bath treatments (Pike & Wadsworth 1999). However, bath treatments might have caused pre-eclosion of nauplii, which could possibly be triggered by changes in osmotic pressure of the fluid within the egg membrane (Gravil 1996, Pike & Wadsworth 1999).

Despite the decreasing number of farmed hosts in Sundalagið, there was a pronounced increase in the abundance of planktonic *L. salmonis*, most of which were nauplii, in March (Fig. 6). The increase co-occurred with the initial warming of the sea water surface (Fig. 2b). The appearance of *L. salmonis* nauplii in the surface water samples in spring agreed with one of the model simulations by Johnsen et al. (2014), which was based on the assumption that nauplii might have the ability to sense temperature and vertically seek warm waters. This would increase their chance of surviving to the copepodid stage, as survival increases with decreasing duration of the nauplii stage. Conversely, the copepodids were not modelled to seek warm waters, since swimming high in the water column increases the chances of intercepting suitable hosts (Heuch et al. 1995, Pike & Wadsworth 1999, Costello 2006).

During winter, when the surface water was colder than the deeper water masses (Fig. 2), *L. salmonis* nauplii were present in only 9% of the 44 samples, while copepodid prevalence was 47%. In the 15 samples where the surface water was vertically the warmest, the prevalence of nauplii increased significantly to 53% ($\chi^2 = 10.9$, df = 1, $p < 0.001$). Copepodid prevalence increased to 60%, but this was not significantly different from the winter situation ($\chi^2 = 2.64$, df = 1, $p = 0.103$). Thus, this study provides field evidence that *L. salmonis* nauplii possibly seek the highest achievable temperature within the water column, and lends support to the assumption of nauplii ability to sense temperature in the model runs of Johnsen et al. (2014).

There was a pronounced seasonal change in *C. elongatus* abundance, from being the dominant planktonic sea louse species during winter to being virtually absent during summer (Fig. 5). The same seasonal changes were also evident in *C. elongatus* on fish farmed in Sundalagið (Fig. 7). This pattern is opposite that which would be expected if productivity were temperature dependent. The pattern is most likely connected to the migration of some unknown fish species, as was also observed in Norway and Scotland (Revie et al. 2002, Øines et al. 2006). However, the timing of infestation in Sundalagið is unlike that in both Scotland and Norway, where infestations occur mainly in summer and early autumn (Revie et al. 2002, Øines et al. 2006).

Despite the limited number of studies on fish abundance in Faroese nearshore waters (Bertelsen 1942, Joensen et al. 2005), there is no doubt that a wide range of *C. elongatus* host species are present in the fjords and straits and even aggregate around fish farms (Dempster et al. 2009). When comparing the population dynamics and migration patterns of the most common fish species in Faroese waters, i.e. mackerel (*Scomber scombrus*), herring (*Clupea harengus*), cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and saithe (*Pollachius virens*), to the population dynamics of *C. elongatus* on farmed salmon, only saithe seems to provide a promising explanation.

Saithe commonly aggregates around fish cages, with the 0-yr group even moving into net pens. Although part of the saithe population is present in the sublittoral zone year round, migration does occur. One-year-old saithe apparently move offshore during summer, as judged by low numbers caught in beach seines (Bertelsen 1942). However, some of the older saithe (1 to 2 yr) re-enter the coastal areas during autumn and winter (Bertelsen 1942, Højgaard 1997). It is possible that migrating saithe carry *C. elongatus* when they enter coastal areas, which might explain the seasonality observed in *C. elongatus* abundance in this study. However, there are many more uninvestigated fish species in Faroese coastal waters, most of which might influence *C. elongatus* abundance on farmed fish.

The ecological consequences of *C. elongatus* facilitated interactions between farmed and wild fish are unknown, and not easily established. In contrast to *L. salmonis*, research on *C. elongatus* is highly sporadic. The latter species should receive much more attention as it might play an important, although yet unknown role in the coastal environment.

In conclusion, this study investigated planktonic stages of sea lice in a region where both *L. salmonis* and *C. elongatus* were abundant, providing insights into the 2 sea lice species simultaneously. The direct observation of the influence of winds on the distribution of *L. salmonis* highlights the importance of including wind patterns in hydrodynamic modelling of the infestation pressure of the species. However, *C. elongatus* was not equally influenced by winds. The vertical migration pattern of planktonic *C. elongatus* is unknown, and it is possible that this pattern could explain the lack of wind influence on the species. Seasonal abundance also differed between the 2 species. *C. elongatus* was highly abundant during winter, but was virtually absent from April to June when the study terminated. *L. salmonis* nauplii abundance increased substantially during early spring when the warmest water was located at the surface as opposed to deeper in the water column. The sudden appearance of nauplii in the warmer surface water could indicate that they seek the highest possible temperature vertically, as this would shorten their development time to the infectious copepodid stage, thereby reducing predation mortality.

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