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Infection of wild fishes by the parasitic copepod *Caligus elongatus* on the south east coast of Norway

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ABSTRACT: Natural *Caligus elongatus* Nordmann infections of wild coastal fishes on the Norwegian south east coast were monitored at various times of the year from 2002 to 2004. The prevalence for all coastal fish (n = 4427) pooled was 15%, and there were great differences between fish species and seasons. Lumpfish *Cyclopterus lumpus* L. spawners were the most infected fish, with a prevalence of 61% and a median intensity of 4 lice fish^{-1}, whereas gadids had a mean prevalence of 19% and a median infection of 1 to 2 lice fish^{-1}. Sea trout *Salmo trutta* L. and herring *Clupea harengus* L. carried *C. elongatus* at prevalence values of 29 and 21%, respectively. The results were compared with infection data for immature North Sea lumpfish. Lumpfish spawners caught on the coast in March to April had fewer lice than North Sea lumpfish in July. Spawners carried mostly adult lice, as did coastal fish hosts in May to June. The low development rates of lice at low spring temperatures and new genetic data suggest that the May to June adult lice could not have been offspring of the March to April lice, indicating transfer of adult lice to coastal fish. Most coastal fish species appeared to acquire new *C. elongatus* infections between May to June and September. The relatively high numbers of chalimii on North Sea lumpfish suggest that offshore fish sustain an oceanic population of this louse species.

KEY WORDS: Infection routes · Sea lice · Lumpfish · Gadidae · Seasons

INTRODUCTION

Caligus elongatus Nordmann, 1832 is probably the most common parasitic copepod in the North Atlantic Ocean (Costello 2006). It is considered to be non-specific, as it can be found on a large number of pelagic and benthic North Sea fishes (Boxshall 1974, Kabata 1979). Normally, the parasite infects its host in the copepodid stage, which subsequently develops in moults through 4 sessile stages, Chalimus 1 to 4, before becoming adult (Piasecki 1996). Unlike its well-known relative the salmon louse *Lepeophtheirus salmonis* Krøyer, *C. elongatus* adults are good swimmers. They are usually attached to their hosts, but may also occur in the plankton (Boxshall 1974, Neilson et al. 1987). Adult lice readily change hosts (Bruno & Stone 1990, Øines et al. 2006). This implies that a fish can be infected independently by both copepodids and adults.

The likelihood of successful transfer between hosts would depend on the density of hosts in the environment (Anderson 1993). The coastal zone is a habitat with a diverse and abundant fish fauna, including resident and migratory species, and *Caligus elongatus* may transfer between these host groups. Residents may be free-swimming or farmed fish, and migrants may travel from oceanic areas into the coastal zone for reproduction or feeding. Currently little is known about the reservoirs and routes of infection underlying sudden rises in *C. elongatus* abundance on coastal fish. It has been proposed that Atlantic salmon *Salmo salar* L. in farms may be infected by adult lice transferring from passing wild hosts (Bron et al. 1993), such as herring *Clupea harengus* or saithe *Pollachius virens* (L.)

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(Wootten et al. 1982). Anecdotal evidence suggests that these infections occur suddenly in the form of adult lice, and that there seems to be no prior build-up of the *C. elongatus* population in the form of juvenile stages. Such a transfer process could explain the marked increases in abundance of adult lice in Scotland from the start of July (Revie et al. 2002).

Which fish species may be reservoirs for such pulse infections in coastal waters? An investigation of the copepod parasites of North Sea fishes caught within 40 miles (~64 km) of the coastal town of Whitby (Yorkshire, UK) showed that all examined lumpfish *Cyclopterus lumpus* L. harboured *Caligus elongatus*, and that the other fish species in the study had a much lower prevalence and mean intensity of this louse (Boxshall 1974). Sea trout *Salmo trutta* L., flounder *Platichthys flesus* (L.), saithe *Pollachius virens* (L.) and pollack *Pollachius pollachius* (L.) carried moderate numbers of *C. elongatus*. Lumpfish spawn on rocky substrates, e.g. in kelp forests, bordering the North Atlantic Ocean (Daborn & Gregory 1983). The adult fish then leave the bottom and return to the plankton, and are transported to the oceanic foraging grounds (Bjelland & Holst 2004). Here, they feed on epipelagic jellyfish, and the populations reach very high densities (Albert et al. 2002, Bjelland & Holst 2004).

In the present work, the possible role of lumpfish, gadids and other hosts in *Caligus elongatus* infection of south east Norwegian coastal fish is evaluated by recording natural prevalence and median intensities of the parasite on a variety of fish species. As lumpfish have previously been found to be a particularly frequently infected host (Boxshall 1974), data on both coastal and North Sea lumpfish infections were collected.

The recent discovery of the 2 distinct genotypes of *Caligus elongatus* (Genotypes 1 and 2; Øines & Heuch 2005, 2007) has now made possible a more detailed study of the infection routes of the parasite. Conveniently, lumpfish had >98 % Genotype 1 lice (Øines & Heuch 2007). The hypotheses in the present work were that lumpfish carry more *C. elongatus* than other fish species, but that gadids and sea trout are also important reservoir hosts for the parasite on the southeast Norwegian coast. The role of lumpfish in the May to June dominance in Genotype 1 *C. elongatus* on coastal fish (Øines & Heuch 2007) is evaluated.

MATERIALS AND METHODS

All sampling was carried out within the same area outside Arendal. The area has no fish farms. A detailed map of the area can be found in Schram et al. (1998). Several different sampling techniques were used to obtain a large variety of fish species and sizes in different habitats. Of the fish in this study, 62 % were caught in a moored bag net. This is an 8 m diameter circular net cage as deep as the depth of water (5.5 m), anchored to the sea floor, with a vertical slit as entrance. The fish meet a 23 m leading net (22 mm bar mesh), which is attached to the shore, and follow this into the entrance, which is extended into the cage in such a way that they will not swim out again. The moored bag net is made of small monofilament mesh net (30 mm bar mesh), which prevents the fish from getting snagged inside the cage. Fishing with this equipment has been described by Dannevig & van der Eyden (1986). The bag net was moored on the inside of the small island of Tjuvholmen (58° 23′ N, 08° 44′ E) in May and August/September, and was emptied every day for 2 to 3 wk. The exact dates for setting and hauling varied somewhat from year to year, as the aim was to fish during periods with a water temperature of >12°C at 19 m depth each year. The net was emptied by carefully hauling up the bottom, so each individual fish could be lifted out with a hand net. They were put in individual plastic bags and brought to the Flødevigen Research Station (FRS) for immediate examination for *Caligus elongatus*. This procedure was followed in 2002, 2003 and 2004.

Spawning lumpfish *Cyclopterus lumpus* were gillnetted in kelp (a mixture of *Laminaria digitata*, *L. saccarina* and *L. hyperborea*) forests at 5 to 20 m depth of water in the Arendal archipelago, no further than 500 m from the coast. Multifilament nets (80 mm stretched mesh size) were fished for about 12 h at night, and the fish were gently removed or cut out from the nets and put into individual plastic bags. The catch was immediately transported to the FRS and examined for *Caligus elongatus*, or frozen for later examination. This sampling was carried out from late February to May. Most fish were caught in March to April.

A beach seine (30 m long, 3.5 m deep, 8 mm mesh size) was used to sample fish in the littoral zone in May to June and September. This equipment was used both on soft and hard bottoms, and always during the day. The seine was rowed out to a depth of approximately 10 m before hauling. Each individual fish was carefully removed from the seine and put in a plastic bag for immediate examination at the FRS. Additional fishing by rod was performed during daytime at depths from 3 to 30 m, in the same area. These fish were only unhooked when in individual plastic bags. The catch was immediately examined at the FRS.

Pelagic lumpfish were caught in July in a pelagic trawl (fishing depth: 0 to 20 m) by the Institute of Marine Research's RV 'G.O. Sars' in the North Sea (57° N, 2 to 6° E). The fish were removed from the trawl when this was on deck, and frozen in plastic bags. This material was thawed and examined for *Caligus elongatus* later.

Chalimii are attached to the fish by a chitinuous thread (Pike et al. 1993), and will therefore rarely be lost. The large volume of the moored bag net and individual extraction of the fish therein would minimise lice loss, whereas the beach seine, gill net and trawl would give a higher risk of detachment. By swift removal and bagging of the individual fish this source of error was kept as small as possible. As all fishing methods involve some risk of lice transfer between hosts or loss of lice to the environment, the recorded adult lice infection intensities must be regarded as minima.

Fish were measured in length to the nearest centimetre and weighed to the nearest gramme. Some very small fish, such as gobies, weighed <1 g, and large variations in stomach content gave a false impression of the actual fish weight. Length was therefore generally chosen as the parameter to describe fish size.

The fish were individually examined while submerged in water in a tray, using large magnifying-glass lamps (Luxo). Only adults and chalimii of the genus *Caligus* were collected. These were identified live as far as possible with a binocular microscope using the descriptions from Kabata (1979), Piasecki (1996) and Schram (1993). Lice from every second infected fish were fixed in 4% formalin, and the lice from the other fish were fixed in 96% ethanol. The formalin-fixed material was stored for verification of species and stage, and for further morphological studies. The ethanol-fixed lice were staged and genetically identified to species by the method of Øines & Heuch (2005) if needed. Other species of *Caligus* were recorded, but for clarity the data are not presented here.

Terms describing the infection follow Bush et al. (1997). Data were entered in a custom-designed Access (Microsoft) database, and analysed using Excel (Microsoft) and JMP (SAS) software. Infection intensities were highly skewed; hence, non-parametric statistics with a significance level of 0.05 were used (Zar 1984). These include median intensity, as a measure of central tendency, and the inter-quartile range (IQR), i.e. the difference between the first and the third quartile, as a measure of variation around the median. The mean abundance is reported in some instances to enable an appreciation of the number of parasites per fish recorded, irrespective of distribution, and for comparison with earlier studies. Mean abundances and lengths were analysed using parametric statistics.

RESULTS

Fish

Altogether, 4427 fish of 52 species caught on the Norwegian south east coast in March to June and September to October from 2002 to 2004 were included in the study. Between March and June 2657 fish were sampled, and 1770 fish were taken in September to October. For 27 species, 10 or more fish were caught (Table 1). For 15 of the species, >100 fish were examined. For comparison with the coastal fish, 73 lumpfish caught in July in the North Sea were included in the study (Tables 1 & 2).

The different gear resulted in the capture of fish of significantly different lengths (ANOVA, $F = 1298$, $p < 0.00001$). Mean (±SD) length of the fish caught in the bag net was 33.4 ± 15.0 cm (n = 2745), in the beach seine it was 7.9 ± 5.6 cm (n = 1378), by rod it was 33.0 ± 12.8 cm (n = 94) and by gill net it was 33.5 ± 10.9 cm (n = 220). The mean length of all fish pooled was 25.4 cm. The North Sea lumpfish *Cyclopterus lumpus* which were caught by surface trawl were immature (cf. Albert et al. 2002). They were significantly smaller than the spawning lumpfish from the coast (*t*-test, $t = 9.9$, $p < 0.0001$; Tables 1 & 2).

Lice

Caligus elongatus infection intensity on coastal fish ranged from 0 to 357 lice individual^{-1}, but 3769 fish carried no lice, giving an overall prevalence of 15%. Of the 27 species listed in Table 1, 21 were infected by *C. elongatus*; in addition, a prevalence of 50% was found on brill *Scophthalmus rhombus* (n = 4, median intensity = 4) and a prevalence of 14.3% was recorded on sea bass *Dicentrarchus labrax* (n = 7, median intensity = 1). On the following 23 fish species, no *C. elongatus* were found: broadnosed pipefish *Syngnathus typhele* (n = 8), cuckoo wrasse *Labrus mixtus* (n = 8), sole *Solea solea* (n = 6), greater pipefish *Syngnathus acus* (n = 5), sea stickleback *Spinachia spinachia* (n = 4), dragonet *Callionymus* sp. (n = 4), great sandeel *Hyperoplus lanceolatus* (n = 3), sprat *Sprattus sprattus* (n = 3), painted goby *Pomatoschistus pictus* (n = 3), sea lamprey *Petromyzon marinus* (n = 3), viviparous blenny *Zoarces viviparus* (n = 3), blue whiting *Micromesistius poutassou* (n = 2), fourhorn sculpin *Triglopsis quadricornis* (n = 2), European hake *Merluccius merluccius* (n = 2), hooknose *Agonus cataphractus* (n = 2), straightnose pipefish *Nerophis ophidion* (n = 2), turbot *Psetta maxima* (n = 1), Nilsson's pipefish *Syngnatus rostellatus* (n = 1), snake pipefish *Entelurus aequoreus* (n = 1), thick-lipped grey mullet *Chelon labrosus* (n = 1), lemon sole *Microstomus kitt* (n = 1), European eel *Anguilla anguilla* (n = 1) and rock gunnel *Pholis gunnellus* (n = 1).

Lumpfish was a particularly heavily infected species; both North Sea and coastal lumpfish had the highest prevalence values and mean abundances (Table 1). One of the North Sea lumpfish had the highest *Caligus elongatus* intensity of all fish in the study, 605 lice. Six lumpfish were caught in the bag net in September

Table 1. Occurrence of *Caligus elongatus* on fish (no. of fish for species with >9 fish) collected at Arendal, Norway, May to June and September 2002 to 2004. Lumpfish from the North Sea were sampled in July. Inter-quartile range (IQR) is the difference between the first and the third quartile. Fish species are ordered by prevalence

Species common name	Scientific name	Number of fish	Fish length (cm) Mean	Fish length (cm) SD	Prevalence (%)	Median intensity	IQR	Abundance Mean	Abundance SD	Fishing gear
Lumpfish, North Sea	*Cyclopterus lumpus*	73	23.2	6.77	83.6	8	19.0	30.5	85.4	Surface trawl
Lumpfish, kelp forest	*Cyclopterus lumpus*	143	31.6	6.12	60.8	4	8.3	7.4	31.3	Gill net, bag net
Tub gurnard	*Cheilidonichtys lucernus*	14	26.6	6.3	50	4	4.5	3.6	7.9	Bag net, beach seine
Pollack	*Pollachius pollachius*	424	35.3	8.2	41	2	2.0	1.2	2.6	Bag net, rod
Sea trout	*Salmo trutta*	268	35.8	8.5	28.8	2	4.0	1.4	4.1	Net, rod, bag net
Herring	*Clupea harengus*	254	27.3	3.5	20.1	1	0.0	0.06	0.3	Bag net
Saithe	*Pollachius virens*	785	26.1	10.1	19.8	1	2.0	0.6	2.0	Bag net, beach seine, rod
Whiting	*Merlangius merlangius*	284	20.6	7.2	16.9	1	1.0	0.2	0.6	Bag net, beach seine
Atlantic cod	*Gadus morhua*	393	21.3	17	12.7	1	1.0	1.2	13.4	Beach seine, gill net
Dab	*Limanda limanda*	11	29.9	10.3	9	1	–	0.1	0.3	Beach seine
Plaice	*Pleuronectes platessa*	13	22.9	9.7	7.7	9	–	0.7	2.7	Bag net
Sand goby	*Pomatoschistus minutus*	127	5.8	1.3	5.5	1	0.0	0.06	0.3	Bag net, beach seine
Two-spotted goby	*Gobiusculus flavescens*	196	3.5	0.6	4.6	1	0.0	0.05	0.4	Beach seine
Mackerel	*Scomber scombrus*	107	32.3	3.7	4.4	1	0	0.07	0.3	Bag net
Poor cod	*Trisopterus minutus*	25	18.3	2.4	4	1	0.0	0.04	0.2	Bag net
Flounder	*Platichthys flesus*	81	30.6	7.8	3.7	1	0.0	0.04	0.2	Bag net, beach seine
Garfish	*Belone belone*	365	64.2	8.3	2.2	0	0.0	0.05	0.4	Bag net
Black goby	*Gobius niger*	90	8.6	2.2	2.2	1	0.0	0.02	0.1	Beach seine
Goldsinny wrasse	*Ctenolabrus rupestris*	207	9.1	2.4	1.9	1	0.0	0.02	0.1	Gill net
Horse mackerel	*Trachurus trachurus*	205	13.1	5.6	1.9	2	2.0	0.05	0.5	Bag net
Transparent goby	*Aphia minuta*	120	4.3	0.6	1.6	1	0.0	0.02	0.1	Bag net
Corkwing wrasse	*Symphodus melops*	108	7.7	4.3	0.9	1	0.0	0.009	0.09	Gill net
Small sandeel	*Ammodytes tobianus*	50	14.7	–	0	0	0.0	0.0	0.0	Beach seine
Ballan wrasse	*Labrus berggylta*	22	20.2	12.2	0	0	0.0	0.0	0.0	Bag net
Three-spined stickleback	*Gasterosteus aculeatus aculeatus*	20	6.4	0.6	0	0	0.0	0.0	0.0	Beach seine
Greater weever	*Trachinus draco*	15	27.1	4.9	0	0	0.0	0.0	0.0	Bag net, beach seine
Rock cook	*Centrolabrus exoletus*	14	5.7	2.4	0	0	0.0	0.0	0.0	Bag net, beach seine
Longspined bullhead	*Taurulus bubalis*	12	13.4	1.6	0	0	0.0	0.0	0.0	Bag net, beach seine

Table 2. Seasonal occurrence of *Caligus elongatus* on lumpfish *Cyclopterus lumpus* caught at Arendal, Norway, by gill net in March to April and by surface trawl in the North Sea in July. IQR: inter-quartile range

Sampling period	Number of fish	Mean weight (g)	Mean length (cm)	Prevalence (%)	Median intensity	IQR	Mean abundance	SD
Mar–Apr 2002	18	1555[a]	31.3[b]	36.8	3	6.0	2.2	5.4
Mar–Apr 2003	83	1023[a]	30.3[b]	60.2	3	10.3	9.5	40.7
Mar–Apr 2004	36	1810[a]	35.1[b]	70.2	5.5	7.8	6.0	9.1
Jul 2002	27	475	21.5	88.9[c]	8[d]	12.8	10.5[e]	11.8
Jul 2003	22	976	25.5	81.8[c]	30[d]	142.0	83.6[e]	14.5
Jul 2004	24	846	23.2	79.2[c]	4[d]	7.0	4.4[e]	5.0

[a]Weight (*t*-test, $t = -4.44$, $p < 0.0001$) and
[b]length (*t*-test, $t = 9.9$, $p < 0.0001$) were significantly higher in the March to April fish.
[c]Prevalence (Fisher exact test, $U = 0.05$, $p = 0.0003$),
[d]intensity (Kruskal-Wallis test with χ^2 approximation, $\chi^2 = 11.15$, $p = 0.0008$) and
[e]abundance (*t*-test, $t = 2.79$, $p = 0.006$) of *C. elongatus* infection were significantly higher for July lumpfish

2003. These had a mean length of 33 cm, a prevalence of *C. elongatus* of 83% and a mean abundance of 4 lice fish^{-1}. These aberrant fish (only included in analyses if specified) were not included in Table 1.

Gadids also occupy a prominent place, as 4 out of the 9 most-infected species belong to this family (Table 1). However, lice prevalence ranged from 13 to 41% on these fishes, and the median intensity of infection only ranged from 1 to 2. The high median intensity of plaice is due to the only infected fish caught, which carried 9 *Caligus elongatus*.

Differences between spring and autumn

Differences between *Caligus elongatus* infections in May to June ('spring') and September ('autumn') were analysed for fish species which included at least 15 fish from each season over the time period of the study. Thirteen species conformed to this heuristic, which excluded lumpfish, since only 6 individual fish of this species were caught in September. Lice prevalence for May to June and September was calculated from all years pooled for each of the 13 fishes (Fig. 1). A Wilcoxon signed-rank test on these pairs showed that the prevalence of lice was significantly lower in May to June (median 6.5) than in September (median 8.1) ($T_+ = 17 < T_{0.05(1)13} = 21$, $p = 0.024$; Zar 1984). Similarly, for the May to June and September data pooled over years, May to June intensities (Kruskal-Wallis test with χ^2 approximation, $\chi^2 = 4.73$, $p = 0.03$) and abundances (*t*-test, $t = 3.38$, $p < 0.0008$; Table 3) were significantly lower than in September. The lice population on the 13 species was divided into 2-stage groups: adults and

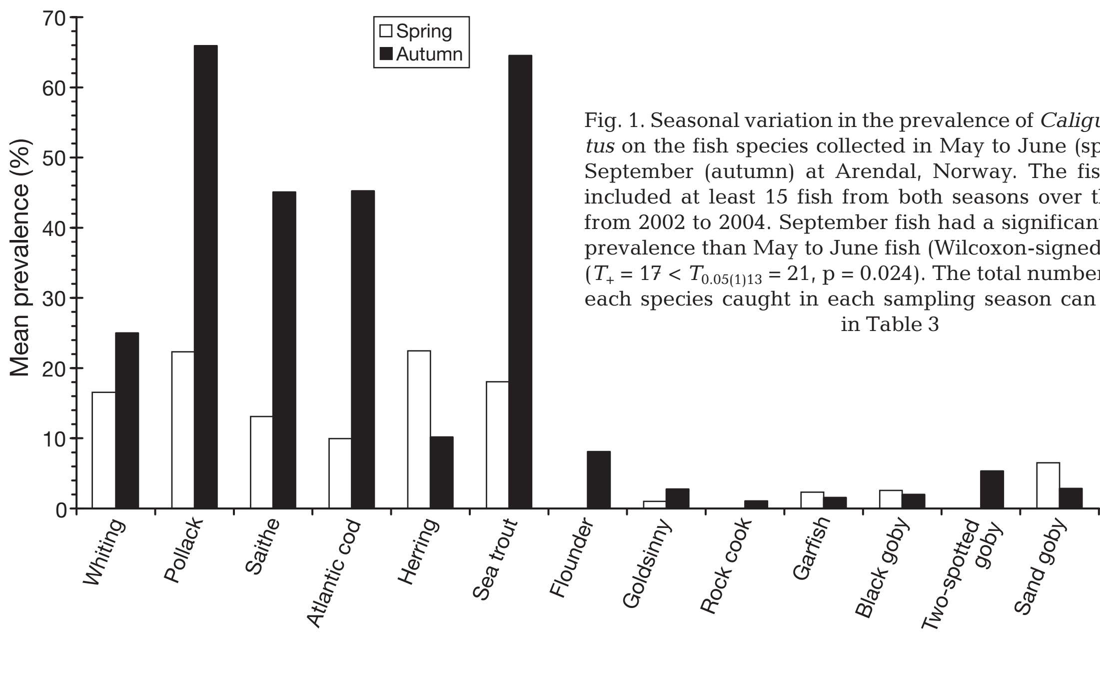

Fig. 1. Seasonal variation in the prevalence of *Caligus elongatus* on the fish species collected in May to June (spring) and September (autumn) at Arendal, Norway. The fish species included at least 15 fish from both seasons over the period from 2002 to 2004. September fish had a significantly higher prevalence than May to June fish (Wilcoxon-signed rank test ($T_+ = 17 < T_{0.05(1)13} = 21$, $p = 0.024$). The total number of fish of each species caught in each sampling season can be found in Table 3

chalimii. May to June fish had 75 to 95% adult lice, and there were 98 to 100% adults in September each year.

Pooled over all examined species, May to June fish had a significantly lower infection intensity of *Caligus elongatus* than September fish (Kruskal-Wallis test with χ^2 approximation, $\chi^2 = 5.11$, $p = 0.024$). The May to June fish had a median intensity of 1 louse (IQR = 2), whereas September fish had a median intensity of 2 lice (IQR = 3). Similarly, the mean abundance of lice for all examined species pooled was significantly lower in May to June (0.19 ± 0.77 SD) than in September (1.16 ± 7.78 SD, *t*-test, $t = 4.57$, $p < 0.0001$).

Prevalence (Fisher exact test, $U = 0.05$, $p = 0.0003$), intensity (Kruskal-Wallis test with χ^2 approximation, $\chi^2 = 11.15$, $p = 0.0008$) and abundance (*t*-test, $t = 2.79$, $p = 0.006$) of *Caligus elongatus* infection on coastal lumpfish in March to April were lower than the values for North Sea lumpfish caught in July (Table 3). Between 35 and 85% of the lice on lumpfish in both habitats were adults.

Variation with fish size

Prevalence of *Caligus elongatus* infection was analysed for the fish species which were caught with both the bag net and beach seine, in numbers above 10 fish per gear type (Table 4). For all 5 species pooled, the fish caught in the bag net were significantly longer than the fish caught by beach seine (*t*-test, $t = 50.03$, $p < 0.0001$), and they had significantly higher prevalence of infection (Fisher exact test, $U = 0.005$, $p = 0.0026$). However, in 2 of the 5 species the prevalence of *C. elongatus* was lower on the larger fish (Table 4). Cod from the seine were only one-sixth of the length of the cod from the bag net, but the prevalence of infection was 100% higher (Table 4).

Lumpfish caught on the coast were significantly larger than North Sea lumpfish (weight *t*-test, $t = -4.44$, $p < 0.0001$; and length *t*-test, $t = 9.9$, $p < 0.0001$), but had significantly lower prevalence, intensity and abundance of *Caligus elongatus* infection.

Genotypes

A mixed Genotype 1 and 2 infection was detected on the lumpfish that were caught in September. Three out of the 7 recorded lice, which were all adults, were Genotype 2 (Øines & Heuch 2007).

Twenty-nine lice from 24 fish smaller than 6 cm, all caught by beach seine, were genotyped according to Øines & Heuch (2007). Of these 29 lice, 19 were sampled in early June, and 18 of them were Genotype 1. These included 16 lice from juvenile Atlantic cod. In September, 8 of 9 lice sampled with this gear were Genotype 2. Two-spotted gobies carried 7 of these 8 lice. No lice from cod of similar size were found in this period. Thus, the genotype pattern of lice from small fish appeared to be similar to the genotype pattern of larger fish (Øines & Heuch 2007).

DISCUSSION

In this study, natural *Caligus elongatus* infections of fishes on the south east Norwegian coast were moni-

Table 3. Summary statistics of *Caligus elongatus* distribution on fish species that were collected in both May to June and September at Arendal, Norway. These species included at least 15 fish from both seasons over the period from 2002 to 2004. Both intensity of infection (*, Kruskal-Wallis test, $\chi^2 = 4.73$, $p = 0.03$) and abundance (**, *t*-test, $t = 3.38$, $p < 0.0008$) were significantly greater in September. IQR: inter-quartile range. For scientific names, see Table 1

Fish species	May–June					September				
	Median intensity	IQR	Mean abundance	SD	n	Median intensity	IQR	Mean abundance	SD	n
Atlantic cod	1	1	0.2	0.5	357	4	14	12.0	43.5	37
Goldsinny wrasse	1	1	0.01	0.1	98	3.5	9	0.02	0.1	109
Sea trout	1	1	0.4	1.0	203	3.5	9	4.6	7.3	65
Pollack	1	1	0.4	0.9	242	2	3	2.3	3.5	182
Sand goby	1	–	0.1	0.2	92	2	–	0.06	0.3	35
Corkwing wrasse	0	–	0.0	–	15	1.1	1	0.01	0.1	93
Flounder	0	–	0.0	–	44	1	0	0.1	0.3	37
Whiting	1	0	0.3	0.4	16	1	1	0.2	0.6	268
Saithe	1	2	0.3	1.1	615	1	3	1.8	4.2	170
Herring	1	1	0.04	0.3	195	1	0.3	0.1	0.4	59
Black goby	1	–	0.03	0.2	40	1	–	0.02	0.1	50
Garfish	2	2	0.5	0.4	301	1	–	0.2	0.1	64
Two-spotted goby	0	0	0.0	0.0	27	0	–	0.08	0.4	169
Pooled	1	0.5	0.19	0.77	2245	1*	1.75	1.15**	7.79	1337

Table 4. *Caligus elongatus*. Comparison of the length and prevalence of *C. elongatus* on fish species that were caught with both bag net and beach seine, and for which at least 10 fish were collected. *: significantly longer fish were sampled with the bag net (t-test, $t = 50.03$, $p < 0.0001$); **: significantly higher prevalence of infection (Fisher exact test, $U = 0.005$, $p = 0.0026$) of fish in bag net

Fish species	Beach seine n	Beach seine Mean length	Beach seine SD	Beach seine Prevalence	Bag net n	Bag net Mean length	Bag net SD	Bag net Prevalence
Saithe	115	10.6	7.6	12.2	619	28.5	7.7	18.9
Whiting	85	10.9	3.9	4.7	186	24.7	3.5	22.6
Atlantic cod	176	5.4	2.5	19.3	155	30.4	8.6	9.0
Flounder	17	22.4	10.1	0.0	60	32.8	5.6	5.0
Corkwing wrasse	87	5.7	1.0	1.1	16	15.8	1.7	0.0
Pooled means		11.0		11.0		26.4*		17.0**

tored in March to April, May to June and September, from 2002 to 2004. The results show that the prevalence for all fish pooled was 15%, and that there were great differences between fish species and seasons. Lumpfish *Cyclopterus lumpus* was the most infected fish species, but gadids also carried significant amounts of *C. elongatus*. The *C. elongatus* infection of lumpfish spawners caught on the coast in March to April was compared with the infection of immature North Sea lumpfish caught in the open sea in July; lumpfish spawners had much lower prevalence and median infection intensity of lice than the immature fish. The prevalence and median intensity of *C. elongatus* infection on most coastal fish species increased between May to June and September. The high number of chalimii on North Sea lumpfish indicates that this louse may reproduce in the ocean. In the following, possible explanations and consequences of the observed infection patterns are discussed in the light of new genetic information (Øines & Heuch 2007).

General patterns of infection

North Sea lumpfish was the fish group most infected by *Caligus elongatus*, followed by the lumpfish caught on the coast. This supports the initial hypothesis that lumpfish is the most infected host species. In the survey of Boxshall (1974) from the English east coast, a 100% prevalence of *C. elongatus* and a mean intensity of 23.2 lice on lumpfish (n = 11) were found. It is, however, not clear whether these fish were caught in the coastal zone or out in the North Sea. As all fish were infected in that survey, the mean intensity was equal to the mean abundance. In the present survey, a prevalence of 84% and a mean abundance of 30.5 lice fish^{-1} were recorded for North Sea lumpfish. Considering the low sample size in the former study, these data are comparable.

Caligus elongatus prevalence on host species sampled on the south east Norwegian coast, excluding lumpfish, ranged from 0 to 50%. Five out of the 15 species with highest prevalence belonged to the Gadidae. For Atlantic cod the prevalence (13%) is similar to observations from the survey of Boxshall (1974), where a research vessel caught Atlantic cod with a *C. elongatus* prevalence of 17%. In the present survey, pollack and whiting had a far higher prevalence than the values recorded by Boxshall (1974), whereas saithe had a much lower prevalence. The present results are congruent with laboratory experiments showing adult lice detached from lumpfish most frequently attach to lumpfish and Atlantic cod, and that adult lice detached from saithe re-attach to this fish, but equally frequently attach to lumpfish (Øines et al. 2006). The hypothesis that gadids are among the most important coastal *C. elongatus* hosts is therefore supported by both laboratory and field data.

Boxshall (1974) found that sea trout carried more *Caligus elongatus* than was found in the present survey, and recorded no lice on North Sea herring. As mentioned above, it is not clear whether these fish were caught in the open ocean. Later observations suggest that herring can carry substantial numbers of *C. elongatus* in the North Sea (MacKenzie & Morrison 1989). A prevalence of approximately 20% was recorded for saithe and herring in coastal waters in the present study. Saithe and herring have been hypothesised to be a source of adult *C. elongatus* in salmon-farming areas (Wootten et al. 1982). Considering the schooling behaviour of these host species, it is possible that adult *C. elongatus* transfer to coastal hosts at a rate that permits their discovery in regular sea lice countings on farms.

Differences between May to June and September samples

Generally, for the fish species that were caught in sufficient numbers both in May to June and September, prevalence and intensity of *Caligus elongatus* were significantly higher in the latter period. A similar pattern has been recorded by a number of authors working with *C. elongatus* data from Atlantic salmon *Salmo salar* L. farms in Scotland (Bron et al. 1993, Stone et al. 2000, Revie et al. 2002), but it was not found in an earlier study by Wootten et al. (1982). Both earlier and later peaks have been observed in Ireland, both in Atlantic salmon farms using treatments against lice (Jackson et al. 2000) and in an untreated farm (Tully 1989). A Canadian study of lice on similar farms suggested peak *C. elongatus* infections in June (Piasecki 1992). The generally low prevalence of lice seen in the May to June coastal fishes (present study) and the fact that approximately 50% of the lice were adults at this time suggest that these fish initially received lice from external sources. However, a small proportion of the lice, including adults, may have survived on coastal fish through the winter.

Sources of lice

Two groups of host fish appeared to be the most important reservoirs of *Caligus elongatus* in the present study: lumpfish and gadids. The former undertakes yearly spawning migrations from the North Sea to coastal areas, such as the south east coast of Norway (Albert et al. 2002, Bjelland & Holst 2004). Lumpfish spawn in the sub-littoral zone (Bjelland & Holst 2004), e.g. in kelp forests. In this habitat resident fish species feed on the rich fauna (Christie et al. 2003, Kelly 2005). Such residents are likely first new hosts for the lice from lumpfish. Sea trout may also be wild natural hosts in coastal marine waters when lumpfish enter these areas in March to April (Heuch et al. 2002).

Genetic studies have shown that 100% of both *Caligus elongatus* on lumpfish caught on the coast in March to April, and on July North Sea lumpfish, are Genotype 1 (Øines & Heuch 2007). In May to June, 91% of other coastal fish have Genotype 1 lice, most of them adults. There is then a genotype shift during summer, whereby the population of *C. elongatus* on coastal fish changes to >90% Genotype 2 lice in September. The small group of aberrant lumpfish caught in September 2003 were the same size as the spawners, and carried a mixed genotype infection (Øines & Heuch 2007). This suggests that they had, contrary to the vast majority of the spent lumpfish, remained in the littoral zone after spawning and thus had been subjected to the increasing Genotype 2 louse infection pressure in summer (Øines & Heuch 2007).

As noted above, there is a possibility that the resident coastal fish caught from May to June had been infected by locally produced Genotype 1 lice earlier the same year. However, as the Genotype 1 population is <10% of the total lice population in autumn (Øines & Heuch 2007), it is likely that the relative contribution of Genotype 1 lice from resident hosts is very small by the end of winter, and the contribution of Genotype 2 lice is correspondingly large. All lice on the lumpfish spawners were Genotype 1, suggesting that they had been carried to the coast by these spawners or other migrant fish.

Tagging of Norwegian coastal Atlantic cod (Moksness & Øiestad 1984, Danielsen & Gjøsæter 1994) and genetic studies (Knutsen et al. 2007) show that these fish have high site fidelity. This suggests that few Atlantic cod from the south east Norwegian coast migrate to open waters and become infected with Genotype 1 *Caligus elongatus*. It seems unlikely that these fish return in numbers that could explain the high rate of infection with Genotype 1 *C. elongatus* in May to June. This is not to say, however, that other migrating fish species do not contribute to the increasing numbers of Genotype 1 lice in May to June. It remains possible, considering the sampling gear, limited areas and time interval between samplings, that fish species not covered in the present survey and by Øines & Heuch (2007) carry significant amounts of *C. elongatus* to the Norwegian south east coast in spring.

Variations in *Caligus elongatus* infection of lumpfish

A reduction of the *C. elongatus* population on lumpfish between July one year and March to April the next year was observed. This decline may be due to a dispersal of lice from spawners, and probably a high mortality in winter and early spring and little development of new adults before or during the migration to the coast. The lower infection intensity of spawning lumpfish compared to North Sea lumpfish supports the hypothesis that adult Genotype 1 lice from spawners infect coastal fish. But it is possible that there is no connection between the lice levels on North Sea lumpfish and spawning lumpfish from the coast. This would be the case if the spawners do not originate from the oceanic lumpfish population from which the immature lumpfish were drawn; or if the lice on the immature lumpfish have developed through one or more generations, all with different survival and speed of development, before being recorded on the coast.

Recent work on lumpfish recruitment in Norwegian waters suggests that the lumpfish caught in the North Sea and on the coast belong to the same population (Albert et al. 2002). Pelagic lumpfish which are 23 cm long in July, as were the pelagic lumpfish in the present study, will most likely grow during autumn and winter to reach maturity and join the spawning stock the year after (Albert et al. 2002). This indicates that

2 fish age groups in the present study are from the same population.

Two lines of evidence indicate that the lice on the 2 groups of lumpfish belong to the same population. First, the lice on both groups are *Caligus elongatus* Genotype 1 (Øines & Heuch 2007). Second, the long development time of the louse at winter temperatures suggests that chalimii found on immature lumpfish at sea in July may have developed to the adults that were found on spawners on the coast from March to April. The total life span of the louse is not known, but even though generation times may be short, adult lice may be long-lived. Piasecki & MacKinnon (1995) suggested a survival time for overwintering adult female *C. elongatus* of ca. 200 d at 2 to 12°C on sea charr *Salvelinus alpinus* L. Similarly, work on the closely related louse *Lepeophtheirus salmonis* shows that adult females can live on the host for half a year at 10°C (Heuch et al. 2000). Tully (1989) estimated the generation time of *C. elongatus* to be between 30 and 60 d on untreated farmed Atlantic salmon in Ireland, whereas Hogans & Trudeau (1989) estimated a generation time of 35 d at 10°C from laboratory cultures. The latter authors also observed a peak of chalimii on farmed salmon on the Canadian east coast in September, and predicted that this group gave rise to a peak in total *C. elongatus* intensity in October. In laboratory cultures other authors have estimated the generation time of *C. elongatus* to be 43 d at 10°C on Arctic charr *Salvelinus alpinus* (Piasecki & MacKinnon 1995). However, recent data on cultured *C. elongatus* copepodids from lumpfish show that the duration of this stage alone may reach 31 d at 12°C (Andersen 2006). This suggests that the entire life span of individual lice is longer than 43 d at 10°C. It is therefore plausible that at least a part of the *C. elongatus* population on the spawning lumpfish are survivors from the North Sea lice population observed the previous year.

Both juvenile lumpfish in the North Sea and spawners arriving at the coast carried chalimii. In the absence of louse survival data from the ocean, it would seem reasonable to assume that these hosts have been infected at sea. Open ocean infection with *Caligus elongatus* has previously been inferred from the observation of chalimii on 0-group haddock and cod on St. Georges Bank in the north east Atlantic (Neilson et al. 1987). Heavy infections with chalimus and adult *C. elongatus* on herring have also been recorded in the North Sea (MacKenzie & Morrison 1989). The abundant lumpfish (Bjelland & Holst 2004), Atlantic salmon (Berland 1993) and other pelagic fish inhabit much the same areas in the Norwegian Sea (Hansen & Jacobsen 2000, Bjelland & Holst 2004), and it is therefore possible that such host fish sustain the complete life cycle of *C. elongatus* here. Furthermore, the oceanic conditions of high salinity and low temperatures will most likely enhance the longevity of the louse (Heuch et al. 2002). Chalimii of the related caligid copepod *Lepeophtheirus salmonis* have also been recorded on Atlantic salmon from the open sea (Jacobsen & Gaard 1997), showing that reproduction of sea lice can occur off-shore.

Summing up, the present data and the results of Øines & Heuch (2007) suggest that the majority of adult lice found on fish on the Norwegian south east coast in May to June originate from the spawning lumpfish, which visited the kelp forests 1 to 2 mo earlier. These lumpfish would be the most important source of lice for coastal fish in spring. These Genotype 1 lice are replaced by Genotype 2 lice during the summer. Most likely, a small proportion of Genotype 2 lice in coastal areas survive the winter, but the already dwindling population of Genotype 1 lice perishes here for unknown reasons. A new supply of Genotype 1 lice would then come with the lumpfish and possibly other fishes arriving at the coast in March to May. Saithe and pollack carry more Genotype 2 lice in spring than do other fish species (Øines & Heuch 2007) and would be likely vectors for this genotype, as they arrive at the coast in early summer. This pattern may not be valid in other areas of Norway, or in other waters.

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