Differences in risks and consequences of salmon louse, *Lepeophtheirus salmonis* (Krøyer), infestation on sympatric populations of Atlantic salmon, brown trout, and Arctic charr within northern fjords

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Differences in salmon louse (*Lepeophtheirus salmonis*) infestation on sympatric populations of fjord-migrating, Atlantic salmon post-smolts (*Salmo salar*), brown trout (*Salmo trutta*) (sea trout), and Arctic charr (*Salvelinus alpinus*) were studied in three fjords with fish-farming activity in northern Norway during the period June–August 2000. Atlantic salmon post-smolts were only captured in the fjords during late June and early July, and probably left them subsequently. No fish were infested with salmon lice. In contrast, brown trout and Arctic charr had similar infection patterns during their sampling periods, with very low prevalence and mean infection intensity during June (0–21% and 0–6 lice per fish, respectively), slightly increasing in July (8–70% and 6–12 lice per fish, respectively), and peaking in August (80–88% and 19–27 lice per fish, respectively). The chalimus stages dominated during June and July, with a few pre-adult and adult stages observed in July, and all stages were found frequently during August. The observations indicate that Atlantic salmon may have a mismatch between the time of louse infestation and their post-smolt fjord migration in northern fjords. In contrast, brown trout and Arctic charr feed within the fjords throughout summer and have a higher risk of harmful infestation in years with suitable environmental conditions for salmon louse development, especially in fish-farming areas. Arctic charr usually spend the shortest time at sea of the three species, and the salmon lice may not have time to develop to the adult stage on this species.

Keywords: anadromy, fish farming, life history, migration, post-smolt, salmonid, salmon lice.

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Introduction

The salmonid species in the northern hemisphere, Atlantic salmon (*Salmo salar* L.), brown trout (*Salmo trutta* L.) (sea trout), and Arctic charr (*Salvelinus alpinus* L.), have an anadromous life-history pattern that utilizes both freshwater and seawater habitats (e.g. Jonsson, 1985; Rikardsen *et al.*, 2000; Klemetsen *et al.*, 2003). The migratory life-history pattern includes major changes in fish physiology and ecology (e.g. Boeuf, 1993; Høgåsen, 1998), exposing the fish to a large variation of environmental and biological challenges. One of these challenges is exposure to the ectoparasitic copepod salmon louse (*Lepeophtheirus salmonis* Krøyer) (Kabata, 1974) in the marine environment (Bakke and Harris, 1998).

Historically, salmon lice have been observed in low numbers on wild salmonids, and few adverse effects on the host have been reported (e.g. Boxshall, 1974; Pemberton, 1976). However, since the late 1980s, there have been heavy infestations of salmon lice on anadromous brown trout (sea trout) along the coast of Norway (Bjørn *et al.*, 2001b), Ireland (Gargan *et al.*, 2003), and Scotland (Butler, 2002). Infested trout, mainly post-smolts, have been reported to be in poor physical condition, some with severely damaged caudal and dorsal fins, and have been observed returning to rivers and estuaries shortly after they have entered the sea (e.g. Birkeland, 1996; Bjørn *et al.*, 2001b). It has been suggested that the increased infestation rate of salmon lice on brown trout is a result of high levels of lice on farmed salmonids in these areas (Tully and Whelan, 1993; Bjørn *et al.*, 2001b; Gargan *et al.*, 2003). Moreover, Norwegian investigations have indicated that lice larvae infest fjord-migrating Atlantic salmon smolt and Arctic charr in areas with salmon farms (Heuch *et al.*, 2005).

The risks and consequences of salmon-louse infestation may, however, vary between species (Bjørn and Finstad, 2002). It will depend on both encounter rate and susceptibility to infestation, as

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well as the different life histories of the fish species (Klemetsen *et al.*, 2003). Given the frequently high numbers of gravid salmon lice carried by the large numbers of cultured fish throughout the year, it is likely that the development of an aquaculture industry has led to changes in the natural host–parasite relationship, and made possible the production of large numbers of infective dispersal louse stages in addition to the natural production of lice on wild salmonids (e.g. Tully and Whelan, 1993; Heuch *et al.*, 2005). As plankton, the lice larvae will drift and be dispersed over long distances, but apparently concentrate near the surface by day (Heuch *et al.*, 1995), and probably also near pycnoclines in stratified waters (Heuch, 1995). The density of infective salmon-louse stages is, therefore, likely to be greatest in the inshore coastal areas and fjords that are subject to constrained tidal flushing. These locations are exploited by feeding and migrating post-smolts, and facilitate increased encounter rates between the parasite and the host.

Their different migrating behaviour at sea may also have strong implications on the risk of salmon-louse infestation. In northern Norway, smolts of anadromous fish migrate to sea for the first time usually during a 2–3 week peak between late May and early July (e.g. Klemetsen *et al.*, 2003; Tuff Carlsen *et al.*, 2004). The timing of this period varies between species and populations, but the final decision when to migrate is determined by environmental factors such as water temperature, light, and water discharge during spring, resulting in annual variation in the peak migration period for each species (Tuff Carlsen *et al.*, 2004). At the same latitude, Arctic charr and brown trout normally spend 1–2 summer months each year at sea before returning to freshwater, where the trout usually return some weeks later than charr (e.g. Jonsson, 1985; Klemetsen *et al.*, 2003). In contrast, Atlantic salmon spend 1–3 years at sea before returning to spawn in freshwater (Klemetsen *et al.*, 2003), and are assumed to move quickly throughout the fjord to the feeding areas in the open sea (Thorstad *et al.*, 2004; Finstad *et al.*, 2005). The three species are therefore subject to different environmental challenges and sources of mortality at sea, including differing susceptibility to salmon louse infestation.

Because of the severe methodological difficulties in capturing Atlantic salmon post-smolts at sea (Holst and McDonald, 2000; Rikardsen *et al.*, 2004), only one previous international, refereed paper reports salmon louse infestation levels in fjord-migrating post-smolts (Finstad *et al.*, 2000). In contrast, there are more infestation data on Arctic charr and especially brown trout (e.g. Tingley *et al.*, 1997; Bjørn and Finstad, 2002), although to the best of our knowledge no study has reported data from sympatric populations of all three species.

The purpose of this study was therefore to investigate the risk of salmon-louse infestation in sympatric populations of fjord-migrating Atlantic salmon, brown trout, and Arctic charr in areas with fish-farming activity in northern Norway. Possible differences in susceptibility between species, the ecological consequences of the infestation, and the relationship with the fish-farming activity are addressed.

Material and methods

Study areas

Three sites in northern Norway were selected for the study: the Altafjord in Finnmark County (Figure 1b), and Malangsfjord and Løksebotten in Troms County (Figure 1a). The Altafjord had

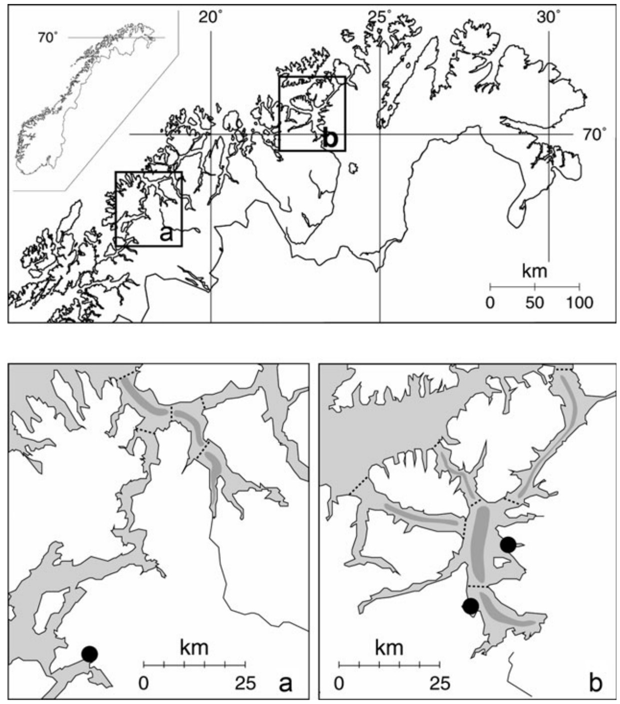

Figure 1. The geographic location of the study in Finnmark and Troms counties, northern Norway. The two counties are shown together with the field locality in (a) Malangsfjord/Løksebotten (69°30′N 18°20′E / 68°55′N 17°41′E) and (b) Altafjord (70°03′N 23°05′E) where fishing was conducted. Atlantic salmon post-smolt trawling was performed in pelagic areas (grey) of different zones (hatched lines) in both Malangsfjord and Altafjord. Sea trout and Arctic charr test-fishing localities in Malangsfjord/Løksebotten and Altafjord are shown by large black dots.

extensive fish-farming activity in 2000, including 17 large salmon farms, and the fjord was classified as relatively intensively farmed (Bjørn *et al.*, 2001a). The inner part of the Malangsfjord system was without fish farms during the study period, and just three fish farms were situated in the outer part of the fjord system. The fjord was therefore classified as having low exposure to fish farming (Bjørn *et al.*, 2001a). Farming activity south of Malangsfjord, especially the area close to Løksebotten, was intensively farmed (Bjørn *et al.*, 2001a). Large populations of Atlantic salmon, sea trout, and Arctic charr are present inside the Altafjord system, and a sampling programme for all three species was established in 2000 (Figure 1b). Atlantic salmon post-smolts were also captured in the Malangsfjord system, and brown trout and Arctic charr from that county were captured in Løksebotten, 70 km south of the Malangsfjord system (Figure 1a). Rikardsen *et al.* (2004) provide further information on the Altafjord and Malangsfjord systems.

Sampling procedures and analyses

Post-smolt Atlantic salmon were captured by a newly developed pelagic trawl, the FISH-lift (Holst and McDonald, 2000), and most of the Arctic charr and brown trout were captured by gillnetting in the littoral zone, as described in Bjørn *et al.* (2001b). The pelagic trawl has proved to be very efficient in capturing fjord-migrating post-smolts, and fish were sampled in two periods during 2000: week 24 and 26 in Malangsfjord and week 25 and 27

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in Altafjord (Rikardsen *et al*., 2004). The fjords were divided into three areas, and several trawls were performed in pelagic areas of the fjords and along the assumed routes of migrating post-smolts (Figure 1a, b). Floating gillnets were set 45–90° to the Altafjord (Figure 1b) and Løksebotten fjord (Figure 1a) shores both day and night to capture brown trout and Arctic charr in their littoral feeding areas in June (week 25/26), July (week 29), and August (week 32/33). The nets were 25 m long and 2 m deep, and had mesh sizes ranging from 19.5 to 35 mm (Bjørn *et al*., 2001b).

All fish were carefully removed from the trawl and the gillnets and immediately placed in individually tagged plastic bags. Weights and total lengths were measured, and the fish were examined for lice under a stereoscope, as described in Bjørn and Finstad (1998). Ecological terms recommended by Bush *et al.* (1997) were used: "prevalence" is defined as the percentage of infested fish, "abundance" is the mean number of parasites per fish caught, "median intensity" is the median number of parasites per infested fish in a sample, and "mean intensity" is the average number of parasites per infested fish. Because of lack of normal distribution and the highly aggregated distributions among the samples, non-parametric Mann–Whitney or Kruskal–Wallis tests were chosen for analyses of statistical differences. Moreover, the variance (s^2) to mean ratio (abundance) was also used to describe the degree of aggregation in the different samples. In all tests, a probability level of $p \leq 0.05$ was considered to be significant.

Fish material

In Altafjord, totals of 47 brown trout, 36 Arctic charr, and 153 Atlantic salmon post-smolts were captured, with average weights of 240 gramme, 360 gramme, and 22 gramme, respectively (Table 1). In Løksebotten and Malangsfjord, the total catch was 24 brown trout, 43 Arctic charr, and 93 Atlantic salmon post-smolts, with average weights of 170 gramme, 260 gramme, and 22 gramme, respectively (Table 1). All brown trout and Arctic charr were captured in the littoral zone, and all Atlantic salmon post-smolts were captured in the pelagic zone of the fjords. The largest fish captured were the few brown trout caught in June in Altafjord. Most of these fish were maturing fish, and most of the other brown trout and Arctic charr captured during the sampling periods were immature fish on their first (post-smolt) or second sea migration. All the Atlantic salmon post-smolts were immature. Overall, Arctic charr were captured most frequently in June and July, and most brown trout in July and August. The Atlantic salmon were captured during early July in Malangsfjord (inner, middle, and outer zones) and Altafjord (inner and middle zones), and some fish were also captured in late June in Malangsfjord (inner zone).

Results

Brown trout and Arctic charr

There were no significant differences in infestation intensity between brown trout and Arctic charr from the same sampling times and locations in June and July (Mann–Whitney *U*-test; $p > 0.05$). The infestation parameters on the two species were therefore pooled to present an overview of salmon-louse infestation among hosts feeding in the littoral zone with time.

Both prevalence and infestation intensity differed significantly between the different sampling periods for brown trout and Arctic charr combined (Kruskal–Wallis; $p < 0.05$), showing much the same general pattern at both localities (Table 2). In June, no brown trout or Arctic charr in the Altafjord had salmon lice, whereas just 21% of the fish in Løksebotten were infested, but at a low rate. In July, just 8% of the fish in Altafjord were infested, and the mean intensity was 12 lice. In contrast, the infestation rate in Løksebotten had increased by July, with a prevalence of 70%, although the mean intensity was similar to that in June (Kruskal–Wallis; $p > 0.05$). However, in August, both prevalence and intensity in both fjords had increased significantly (Kruskal–Wallis; $p < 0.05$). In Løksebotten, 80% of the fish were infested, and the mean intensity was 27 lice, and 88% of the fish from Altafjord were infested, with a mean intensity of 19 lice. Maximum values in Løksebotten and Altafjord were 59 and 78 lice, respectively.

In general, the chalimus stages dominated during June and July, but with a few pre-adult and adult stages in July (especially in Løksebotten), whereas all stages were more frequent during the peak in August (Figure 2). In Altafjord in July, few early (I and II) and late chalimus (III and IV) stages dominated, but a few adult male lice were found on the fish (Figure 2a). In August, more especially early and late chalimus stages were found, but there had also been an aggregation of older louse stages on the fish in Altafjord. The louse population on fish from Løksebotten was dominated by a few chalimus stages in June (Figure 2b). The chalimus infestation had slightly increased there in July, and older stages also aggregated on the fish. In August, there was a new infestation of louse larvae in Løksebotten, but also a significant aggregation of older lice on the fish.

The relative intensity, i.e. the number of lice per gramme fish weight, in fish from Løksebotten also increased significantly

Table 1. Fish sampled in the Altafjord (Atlantic salmon, brown trout, and Arctic charr), in the Malangsfjord (Atlantic salmon), and at Løksebotten (brown trout and Arctic charr).

Species	Week	Altafjord	Malangsfjord/Løksebotten
Brown trout	25/26 (June)	626.3 ± 645.0 (6)	61.0 ± 16.9 (3)
Arctic charr		338.6 ± 150 (14)	220.9 ± 206.2 (21)
Atlantic salmon		(0)	23.1 ± 5.2 (10)
Brown trout	29 (July)	202.3 ± 213.7 (22)	245.3 ± 342.57 (11)
Arctic charr		407 ± 449.7 (15)	289.3 ± 116.3 (22)
Atlantic salmon		22.4 ± 4.6 (153)	22.1 ± 6.7 (83)
Brown trout	32/33 (August)	161.7 ± 122.3 (19)	134 ± 74 (10)
Arctic charr		296.7 ± 260.2 (7)	(0)
Atlantic salmon		–	–

The mean weight ± standard deviation and the number (*n*) of Atlantic salmon, brown trout, and Arctic charr in each sampling week are given.

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Table 2. Infestation intensity on pooled groups of brown trout and Arctic charr from the Altafjord and Løksebotten in June (25 and 26), July (29), and August (32 and 33).

Sampling week	Habitat	*n*	Prev	Mean	s.d.	Median	IQR	Min	Max	s^2/x
Altafjord										
26 (June)	SW	20	0	–	–	–	–	–	–	–
29 (July)	SW	37	8.1	12	13	–	–	4	27	14
32 (August)	SW	26	88.4	18.9	18.6	14	22	1	78	18.3
Malangsfjord/ Løksebotten										
25 (June)	SW	24	20.8	6.4	4.6	5	8.5	1	13	3.4
29 (July)	SW	33	69.7	5.9	5.9	4	6	1	25	5.7
33 (August)	SW	10	80	26.5	22.3	24.5	46	4	59	18.7

n is the total number of fish captured, Prev the percentage of infested fish in the total number of fish, Mean the mean numbers of lice on infested fish only (intensity), s.d. the standard deviation, IQR the interquartile range, Min and Max are the minimum and maximum number of lice, s^2/x is the variance to mean ratio, and SW is saltwater.

during the sampling period (Kruskal–Wallis; $p < 0.05$; Figure 3). In June and July relative intensities were very low, and the levels peaked in August at median levels close to 0.2 lice per gramme fish weight. In the Altafjord system, approximately similar median relative intensities (0.15 lice per gramme fish weight) were found in July and August, but relatively few individuals were infested early in the season, in contrast to most of the population in August. The maximum value in Altafjord was 0.7 lice per gramme fish weight. In Løksebotten, approximately 25% of all infested post-smolts carried relative intensities between 0.15 and 0.7 lice per gramme fish weight in August.

Atlantic salmon

No salmon lice were found on pelagic, captured, post-smolt Atlantic salmon from the Altafjord and Malangsfjord in any of the sampling periods in late June and early July, which is quite different from the situation described for sea trout and Arctic charr captured in the littoral zone (Table 2). This statement includes the few fish captured in the inner zone of Malangsfjord in late June, and in the inner, middle, and outer zone of the fjord in July (week 27). The same pattern was found for post-smolts in the Altafjord system, captured in the inner zone in June and in the middle zone in July: no fish were captured in the outer zone in this fjord.

Discussion

Clearly, the risks of salmon-louse infestation may differ between sympatric populations of Atlantic salmon post-smolts, brown trout, and Arctic charr in north Norwegian fjords, and this may be explained by generic differences in their marine life history, including migration timing, behaviour, and the duration of fjord residence.

In the Altafjord, brown trout and Arctic charr captured in the littoral zone and pelagic-captured Atlantic salmon post-smolts were uninfested with salmon lice in late June. The same pattern was found for Atlantic salmon post-smolts from Malangsfjord in late June, and only a few lice were found on littoral-feeding Arctic charr and brown trout from Løksebotten during the same period. In July, more than two-thirds of the brown trout and Arctic charr in Løksebotten were infested, whereas fewer than 10% of the Arctic charr and brown trout in Altafjord were infested with just a few salmon lice. No Atlantic salmon post-smolts were infested in any of the fjords during the same period, and the post-smolts of this species had probably left the fjord during late July. However, in the middle of August (week 32/33) the louse infestation on brown trout and Arctic charr had increased dramatically, and there was an epidemic tendency through the concurrent rise in prevalence, intensity, and variance to mean ratio in both systems. This pattern of infestation is to a large extent consistent with earlier studies in northern areas, where the infestation pressure usually increased in August after relatively low levels in June and July (Bjørn and Finstad, 2002). There are, however, also variations between years, and increased infestation pressure has also been observed in early July in both Altafjord (Bjørn and Finstad, 2002) and at different localities in Troms County (Bjørn *et al.*, 2000).

Although the sampling periods for Atlantic salmon post-smolts were not completely comparable with those of Arctic charr and brown trout because of small differences in sampling time and space, the results indicate that a difference in risks of infestation may exist between pelagic, migratory, Atlantic salmon post-smolts and the littoral fjord-feeding brown trout and Arctic charr. The infestation pattern in brown trout and Arctic charr showed a remarkable similarity between localities: very low infestations in June, increased prevalence in July, and a peak in both prevalence and mean intensity in August, at levels significantly higher than assumed historical ones (e.g. Boxshall, 1974; Pemberton, 1976) and in areas without fish farms in recent years (Tingley *et al.*, 1997; Mo and Heuch, 1998; Rikardsen, 2004).

The relationship between the growth of the fish-farming industry along the coast and salmon lice attacks on both farmed and wild salmonids has been discussed in recent years (Pike and Wadsworth, 1999; Tully and Nolan, 2002; Heuch *et al.*, 2005). Direct evidence of louse transfer from farmed to wild hosts has, however, not been found. There is, however, substantial evidence indicating that infesting copepodids from salmon lice on farmed fish have a role in generating the epidemics observed on wild salmonids in farming areas (Bjørn *et al.*, 2001b; Gargan *et al.*, 2003; Krkošek *et al.*, 2005). Historical infestation levels on brown trout (Boxshall, 1974), and infestation levels in areas without fish farming, are generally at a relatively high prevalence but low intensity (e.g. Tingley *et al.*, 1997; Rikardsen, 2004). The variability between years also seems to be low in areas with no fish-farm activity, probably representing a stable long-term situation with few adult lice, low transmission rates, and no adverse effect on the fish (Tingley *et al.*, 1997; Schram *et al.*, 1998; Rikardsen, 2004).

Within Atlantic salmon farms, or within fish-farming areas, large numbers of hosts are continually present, facilitating the build-up of a large number of reproducing female lice and a

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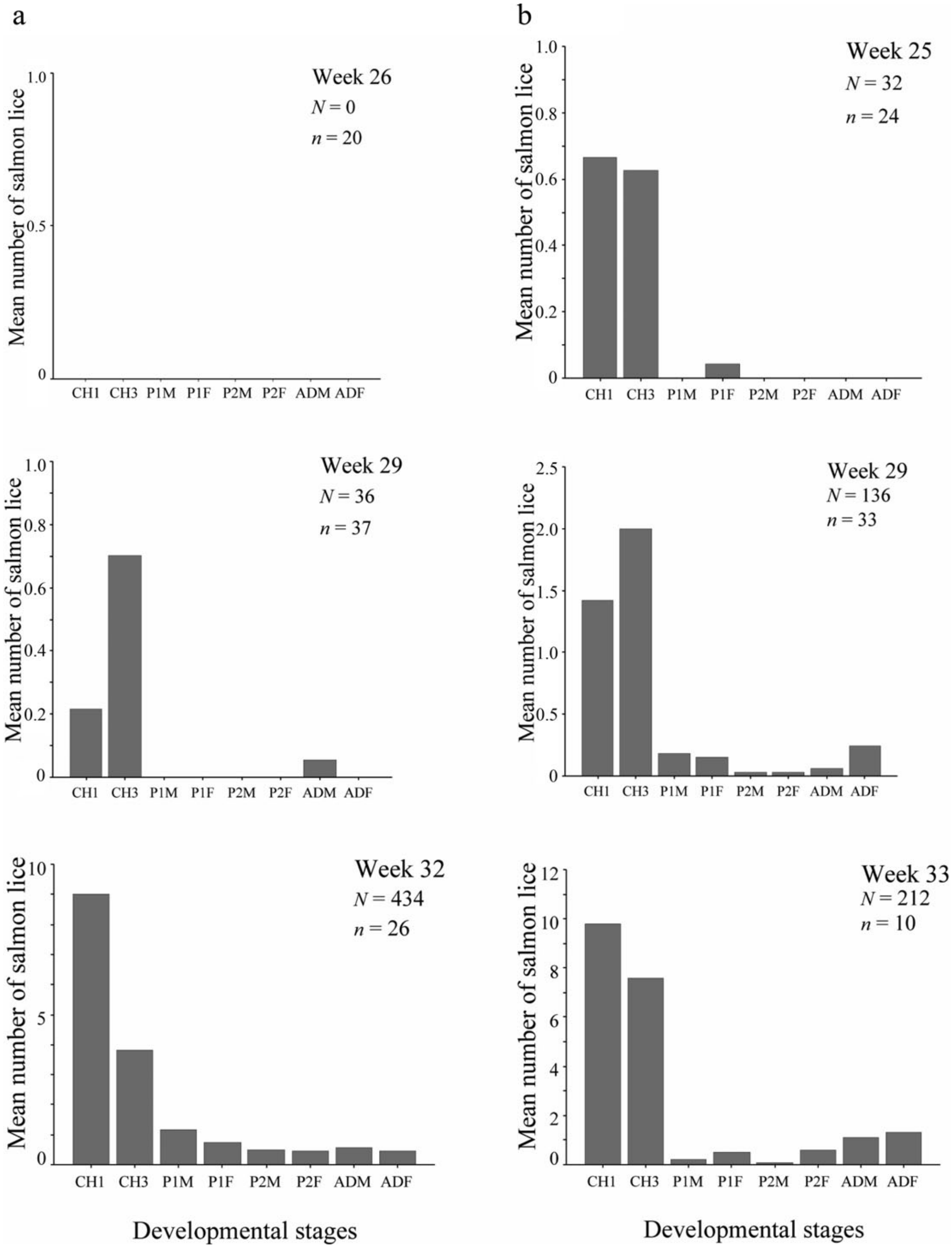

Figure 2. Distribution of the developmental stages (%) of salmon lice on pooled groups of sea trout and Arctic charr captured in salt water in (a) Altafjord and (b) Malangsfjord/Løksebotten. The fish were sampled in June (week 25/26), July (week 29), and August (week 32/33). *N* is the total number of lice on the fish and *n* is the number of fish sampled. Developmental stages are designated as follows: CH1, first and second chalimus stage combined; CH3, third and fourth chalimus stage combined; P1M, first pre-adult male; P1F, first pre-adult female; P2M, second pre-adult male; P2F, second pre-adult female; ADM, adult male; ADF, adult female.

continuous possibility of re-infestation (e.g. Tully and Whelan, 1993; Heuch and Mo, 2001). As the potential for larva production is substantially higher under marine cage-culture conditions (Heuch *et al.*, 2005), years with optimal conditions for louse reproduction and dispersal may potentially result in salmon-louse epidemics in wild salmonids (Bjørn *et al.*, 2001b, Stien *et al.*, 2005). At least in brown-trout populations, these epidemics are characterized by high infestation pressure leading to physiological damage, or even lethal louse-infestation levels, a premature return to freshwater of the most heavily infested fish, and indices of direct parasite-induced mortality of heavily infested fish (Bjørn *et al.*, 2001b). The risks of infestation from free-swimming

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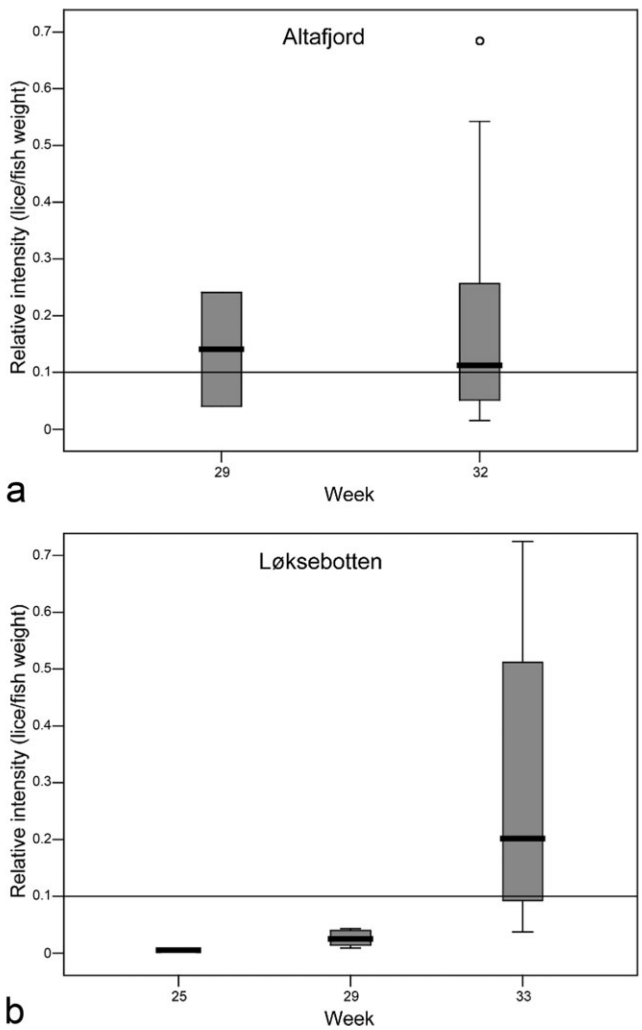

Figure 3. Box-and-whisker plot showing the relative intensity of lice (number of lice per gramme fish weight) on the smallest fish (<200 g) in (a) Altafjord in July (week 29; *n* 2) and August (week 32; *n* 17) and (b) Løksebotten in June (week 25; *n* 1), July (week 29; *n* 8) and August (week 33; *n* 8). Horizontal lines indicate medians. The lower and upper hinges give the 25th and 75th percentile. Outliers (o) are presented, and the whiskers give the largest and smallest observed values that are not outliers. The horizontal line gives the relative intensity expected to cause minor osmoregulatory disturbances of the fish (Wagner *et al.*, 2003, 2004).

salmon-louse copepodids derived from cultured fish to wild salmonids will depend on such factors as the number and dispersal of lice from fish farms, the behaviour, survival, and longevity of infesting copepodids (Stien *et al.*, 2005), and the feeding or migratory areas of wild salmonids in relation to farms (Thorstad *et al.*, 2004; Rikardsen *et al.*, in press).

The risks of salmon-louse infestation may, therefore, also differ between salmonid species, as is indicated by the results of the present study, and may also differ from the infestation risk in areas to the south. Results from Bjørn and Finstad (1998) imply, although they were not directly tested, that salmon lice have a similar development and growth rate on the congeneric brown trout, Arctic charr, and Atlantic salmon, compared with the Pacific salmon species *Oncorhynchus* spp. (Johnson and Albright, 1992; Johnson, 1993). Similar results have also been indicated from field studies, in which brown trout and Arctic charr have both become heavily infested with salmon lice when feeding in fjords and coastal areas of intensive fish-farming activity (Bjørn *et al.*, 2001b; Bjørn and Finstad, 2002). Fjord-migrating post-smolts of Atlantic salmon have been found with low levels of salmon-louse infestation in fjords almost without fish-farming activity (Finstad *et al.*, 2000), but dramatically high infestation rates have also been found in post-smolts descending from intensively farmed areas of western Norway (Heuch *et al.*, 2005).

The marine migratory behaviour of Atlantic salmon, Arctic charr, and brown trout diverge in several important aspects, although knowledge of the detail is still limited. Most of the information gathered to date suggests that post-smolt Atlantic salmon move relatively quickly through estuaries and fjords close to the surface (e.g. Moore *et al.*, 2000; Thorstad *et al.*, 2004), although this also may vary between populations and years (Rikardsen *et al.*, 2004). In contrast, brown trout and Arctic charr usually feed in littoral areas close to their native river throughout summer and autumn (Berg and Jonsson, 1990; Lyse *et al.*, 1998; Rikardsen *et al.*, 2000). Tagging experiments using data-logger tags on trout and charr have shown that the fish spend more than 90% of the time within 3 m of the surface in Altafjord (Rikardsen *et al.*, in press). Brown trout and Arctic charr therefore seem to belong to a "near shore, surface-orientated guild of fishes" as previously suggested by Grønvik and Klemetsen (1987), although these fish may also occasionally feed pelagically in open water within fjords (Rikardsen and Amundsen, 2005). Fish farms are usually located close to the littoral zone. Infesting dispersal stages of salmon lice may therefore be more concentrated nearshore and in fjords and lochs with a turbulent current pattern and often distinct thermoclines and haloclines, which seem to be the preferred areas of both brown trout and Arctic charr (e.g. Lyse *et al.*, 1998; Rikardsen *et al.*, 2000), as well as for salmon-louse copepodids (e.g. Heuch *et al.*, 1995; McKibben and Hay, 2004).

There are also differences in the timing of migration between species; often large, veteran Arctic charr descend prior to veteran brown trout, followed by smolts of Atlantic salmon, Arctic charr, and brown trout (Tuff Carlsen *et al.*, 2004). Similarly, there are also differences in the seawater residence of Arctic charr and brown trout within fjords. Arctic charr usually ascend earlier than brown trout in late summer or autumn, where large veteran Arctic charr dominate among the early ascenders while post-smolts return later (Berg and Jonsson, 1990; Rikardsen *et al.*, 1997). Moreover, some brown trout are also known to stay in seawater during late autumn and winter within some northern fjords (Rikardsen, 2004). In addition to possible immunological differences between salmonid species (Dawson *et al.*, 1997), these behavioural differences may lead to different risks of infestation. Furthermore, the seawater temperature is usually much lower in the northern than in the southern fjords of Norway (Rikardsen *et al.*, 2004). As a result, the peak in infestation pressure is often on trout and charr in the period August–October in northern latitudes (Bjørn and Finstad, 2002) compared with the period June–August in more southern latitudes (Schram *et al.*, 1998; Heuch *et al.*, 2005). Usually, Atlantic salmon post-smolts have left the northern fjord (Rikardsen *et al.*, 2004) by the time infestation pressure is at its highest. Hence, they may experience "mismatch" conditions in northern fjords between the peak in infestation risk and their normal migration period. This may also be the case for veteran migrant brown trout, and especially Arctic charr veterans

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that often ascend the rivers in July or early August (Berg and Jonsson, 1990). Immature Arctic charr and brown trout often stay longer in seawater (Berg and Jonsson, 1990), and some brown trout may even spend the whole autumn and winter at sea (Rikardsen, 2004). Immature brown trout especially may therefore often take on high salmon-louse infestations, and results from this study as well as previous results from the Altafjord system (Bjørn and Finstad, 2002) indicate that relative infestation intensities reach levels that may impair fish physiology (e.g. Bjørn and Finstad, 1997; Nolan *et al*., 1999; Wagner *et al*., 2003). The August infestation levels found on the most heavily infested small brown trout from both Altafjord and Løksebotten may therefore have consequences for the population in the longer term (Tully and Nolan, 2002; Heuch *et al*., 2005). In contrast, Arctic charr may spend too short a time at sea (average 30–50 d; e.g. Finstad and Heggberget, 1993; Rikardsen, 2000) for the salmon lice to develop to the more harmful, mobile, pre-adult and adult stages, although severe and harmful levels of infestation have also been observed on this species as well in some years. However, knowledge of the early marine ecology of salmonids is still limited. For example, recent results from the Altafjord indicate prolonged feeding of Atlantic salmon post-smolts on energy-rich fish larvae within the fjord system (Rikardsen *et al*., 2004; Knudsen *et al*., 2005). If that is the case, the risks of salmon-louse infestation may be severely increased in northern areas also. This and other aspects of the marine migratory behaviour of the three salmonids investigated here should be addressed carefully in order to reduce the risk of salmon-louse infestation from the burgeoning fish-farming industry in northern latitudes. Additionally, a single low limit for the maximum legal mean number of lice per farmed fish from spring to autumn (Heuch *et al*., 2005) is required to protect immature brown trout especially from the August peak in infestation risk.

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References

Bakke, T. A., and Harris, P. D. 1998. Diseases and parasites in wild Atlantic salmon (*Salmo salar*) populations. Canadian Journal of Fisheries and Aquatic Sciences, 55 (Suppl. 1): 247–266.

Berg, O. K., and Jonsson, B. 1990. Growth and survival rates of the anadromus trout, *Salmo trutta*, from the Vardnes River, northern Norway. Environmental Biology of Fishes, 29: 145–154.

Birkeland, K. 1996. Consequences of premature return by sea trout (*Salmo trutta)* infested with the salmon lice (*Lepeophtheirus salmonis* Krøyer): migration, growth and mortality. Canadian Journal of Fisheries and Aquatic Sciences, 53: 2808–2813.

Bjørn, P. A., and Finstad, B. 1997. The physiological effects of salmon lice infection on sea trout post smolts. Nordic Journal of Freshwater Research, 73: 60–72.

Bjørn, P. A., and Finstad, B. 1998. The development of salmon lice (*Lepeophtheirus salmonis*) on artificially infected sea trout (*Salmo trutta*) post smolts. Canadian Journal of Zoology, 76: 970–977.

Bjørn, P. A., and Finstad, B. 2002. Salmon lice, *Lepeophtheirus salmonis* (Krøyer), infestation in sympatric populations of Arctic char, *Salvelinus alpinus* (L.), and sea trout, *Salmo trutta* (L.), in areas near and distant from salmon farms. ICES Journal of Marine Science, 59: 131–139.

Bjørn, P. A., Finstad, B., and Kristoffersen, R. 2001b. Salmon lice infections of wild sea trout and Arctic char in marine and freshwaters: the effects of salmon farms. Aquaculture Research, 31: 795–803.

Bjørn, P. A., Kristoffersen, R., and Finstad, B. 2000. Lakselus på vill sjøørret og sjørøye i Troms sommeren 1999 [Salmon lice on wild sea trout and Arctic charr in Troms in summer 1999]. – Rapport til Fiskehelse og Miljøgruppa i Troms, Fiskeridirektoratet, region Troms. 34 pp. (in Norwegian).

Bjørn, P. A., Kristoffersen, R., and Finstad, B. 2001a. Registreringer av lakselus på laks, sjøørret og sjørøye i 2000. [Registrations of salmon lice on Atlantic salmon, sea trout and Arctic charr in 2000]. NINA Oppdragsmelding, 698. 40 pp. (in Norwegian with English summary).

Boeuf, G. 1993. Salmonid smolting: a preadaptation to the oceanic environment. *In* Fish Ecophysiology, pp. 105–135. Ed. by J. C. Rankin, and F. B. Jensen. Chapman and Hall, London.

Boxshall, G. A. 1974. Infection with parasitic copepods in North Sea marine fishes. Journal of the Marine Biological Association of the UK, 54: 355–372.

Bush, A. O., Lafferty, K. D., Lotz, J. M., and Shostak, A. W. 1997. Parasitology meets ecology on its own terms: Margolis *et al*. revised. Journal of Parasitology, 83: 575–583.

Butler, J. R. A. 2002. Wild salmonids and sea louse infestations on the west coast of Scotland: sources of infection and implications for the management of marine salmon farms. Pest Management Science, 58: 595–608.

Dawson, L. H. J., Pike, A. W., Houlihan, D. F., and McVicar, A. H. 1997. Comparison of the susceptibility of sea trout (*Salmo trutta* L.) and Atlantic salmon (*Salmo salar* L.) to sea lice (*Lepeophtheirus salmonis* (Krøyer, 1837)) infections. ICES Journal of Marine Science, 54: 1129–1139.

Finstad, B., Bjørn, P. A., Grimnes, A., and Hvidsten, N. A. 2000. Laboratory and field investigations of salmon lice [*Lepeophtheirus salmonis* (Krøyer)] infestation on Atlantic salmon (*Salmo salar* L.) postsmolts. Aquaculture Research, 31: 795–803.

Finstad, B., and Heggberget, T. G. 1993. Migration, growth and survival of wild and hatchery-reared anadromous Arctic charr (*Salvelinus alpinus*) in Finnmark, northern Norway. Journal of Fish Biology, 43: 303–312.

Finstad, B., Økland, F., Thorstad, E. B., Bjørn, P. A., and McKinley, R. S. 2005. Migration of hatchery-reared Atlantic salmon and wild sea trout post-smolts in a Norwegian fjord system. Journal of Fish Biology, 66: 86–96.

Gargan, P. G., Tully, O., and Poole, W. R. 2003. Relationship between sea lice infestation, sea lice production and sea trout survival in Ireland, 1992–2001. *In* Salmon at the Edge, pp. 119–135. Ed. by D. Mills. Blackwell Science, Oxford.

Grønvik, S., and Klemetsen, A. 1987. Marine food and diet overlap of co-occurring Arctic charr *Salvelinus alpinus* (L.), brown trout *Salmo trutta* L. and Atlantic salmon *S. salar* L. off Senja, N. Norway. Polar Biology, 7: 73–177.

Heuch, P. A. 1995. Experimental evidence for aggregation of salmon louse copepodids, *Lepeophtheirus salmonis*, in step salinity gradients. Journal of the Marine Biological Association of the UK, 75: 927–939.

Heuch, P. A., and Mo, T. A. 2001. A model of salmon louse production in Norway: effects of increasing salmon production and public management measures. Diseases of Aquatic Organisms, 45: 145–152.

Heuch, P. A., Bjørn, P. A., Finstad, B., Holst, J. C. H., Asplin, L., and Nilsen, F. 2005. A review of the Norwegian "National Action Plan Against Salmon Lice on Salmonids": the effects on wild salmonids. Aquaculture, 246: 79–92.

Heuch, P. A., Parsons, A., and Boxaspen, K. 1995. Diel vertical migration: a possible host-finding mechanism in salmon louse

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(*Lepeophtheirus salmonis*) copepodids? Canadian Journal of Fisheries and Aquatic Sciences, 52: 681–689.

Holst, J. C., and McDonald, A. 2000. FISH-LIFT: a device for sampling live fish with trawls. Fisheries Research, 48: 87–91.

Høgåsen, H. R. 1998. Physiological changes associated with the diadromous migration of salmonids. Canadian Special Publications in Fisheries and Aquatic Sciences, 127. 128 pp.

Johnson, S. C. 1993. A comparison of development and growth rates of *Lepeophtheirus salmonis* (Copepoda: Caligidae) on naïve Atlantic (*Salmo salar)* and chinook (*Oncorhynchus tshawytscha)* salmon. *In* Pathogens of Wild and Farmed Fish: Sea Lice, pp. 68–80. Ed. by G. A. Boxhall, and D. Defaye. Ellis Horwood, London.

Johnson, S. C., and Albright, L. J. 1992. Comparative susceptibility and histopathology of the response of naive Atlantic, chinook and coho salmon to experimental infection with *Lepeophtheirus salmonis* (Copepoda: Caligidae). Diseases of Aquatic Organisms, 14: 179–193.

Jonsson, B. 1985. Life history patterns of freshwater resident and sea-run migrant brown trout in Norway. Transactions of the American Fisheries Society, 114: 182–194.

Kabata, Z. 1974. Mouth and mode of feeding of Caligidae (Copepoda), parasites of fishes, as determined by light and scanning electron microscopy. Journal of the Fisheries Research Board of Canada, 31: 1583–1588.

Klemetsen, A., Amundsen, P.-A., Dempson, B., Jonsson, B., Jonsson, N., O'Connell, M. F., and Mortensen, E. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecology of Freshwater Fish, 12: 1–59.

Knudsen, R., Rikardsen, A. H., Dempson, J. B., Bjørn, P. A., Finstad, B., Holm, M., and Amundsen, P-A. 2005. Trophically transmitted parasites in wild Atlantic salmon post-smolts from Norwegian fjords. Journal of Fish Biology, 66: 1–15.

Krkošek, M., Lewis, M. A., and Volpe, J. P. 2005. Transmission dynamics of parasitic sea lice from farm to wild salmon. Proceedings of the Royal Society, Series B, 272: 689–696.

Lyse, A. A., Stefansson, S. O., and Fernö, A. 1998. Behaviour and diet of sea trout post-smolt in a Norwegian fjord system. Journal of Fish Biology, 52: 923–936.

McKibben, M. A., and Hay, D. 2004. Distribution of planktonic sea lice larvae *Lepeophtheirus salmonis* in the inter-tidal zone in Loch Torridon, western Scotland in relation to salmon farm production cycles. Aquaculture Research, 35: 742–750.

Mo, T. A., and Heuch, P. A. 1998. Occurrence of *Lepeophtheirus salmonis* (Copepoda: Caligidae) on sea trout (*Salmo trutta*) in the inner Oslo Fjord, south-eastern Norway. ICES Journal of Marine Science, 55: 176–180.

Moore, A., Lacroix, G. L., and Sturlaugsson, J. 2000. Tracking Atlantic salmon post-smolts in the sea. *In* The Ocean Life of Atlantic Salmon – Environmental and Biological Factors Influencing Survival, pp. 49–64. Ed. by D. Mills. Fishing News Books, Oxford.

Nolan, D. T., Reilly, P., and Wendelaar Bonga, S. E. 1999. Infection with low numbers of the sea louse *Lepeophtheirus salmonis* induces stress-related effects in postsmolt Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences, 56: 947–959.

Pemberton, R. 1976. Sea trout in the North Argyll sea lochs: population, distribution, and movements. Journal of Fish Biology, 9: 157–179.

Pike, A. W., and Wadsworth, S. L. 1999. Sealice on salmonids: their biology and control. Advances in Parasitology, 44: 233–337.

Rikardsen, A. H. 2000. Effects of Floy and soft VI alpha tags on growth and survival of juvenile Arctic char. North American Journal of Fisheries Management, 20: 719–728.

Rikardsen, A. H. 2004. Seasonal occurrence of salmon lice *Lepeophtheirus salmonis* on sea trout *Salmo trutta* in north Norwegian fjords without fish farms. Journal of Fish Biology, 65: 711–722.

Rikardsen, A. H., and Amundsen, P-A. 2005. Pelagic marine feeding behaviour of Arctic charr *Salvelinus alpinus* and sea trout *Salmo trutta*. Journal of Fish Biology, 66: 1163–1166.

Rikardsen, A. H., Svenning, M-A., and Klemetsen, A. 1997. The relationships between anadromy, sex ratio and parr growth of Arctic charr in a lake in north Norway. Journal of Fish Biology, 51: 447–461.

Rikardsen, A. H., Amundsen, P-A., Bjørn, P. A., and Johansen, M. 2000. Comparison of growth, diet and food consumption of sea-run and lake-dwelling Arctic charr. Journal of Fish Biology, 57: 1172–1188.

Rikardsen, A. H., Diserud, O. H., Elliott, J. M., Dempson, B., Sturlaugsson, J., and Jensen, A. M. The marine temperature and depth preferences of Arctic charr and sea trout, as recorded by data storage tags. Fisheries Oceanography (in press).

Rikardsen, A. H., Haugland, M., Bjørn, P. A. Finstad, B., Knudsen, R., Dempson, B., and Holm, M. 2004. Geographical differences in early marine feeding of Atlantic salmon post-smolts in Norwegian fjords. Journal of Fish Biology, 64: 1655–1679.

Schram, T. A., Knutsen, J. A., Heuch, P. A., and Mo, T. A. 1998. Seasonal occurrence of *Lepeophtheirus salmonis* and *Caligus elongatus* (Copepoda: Caligidae) on sea trout (*Salmo trutta*), off southern Norway. ICES Journal of Marine Science, 55: 163–175.

Stien, A., Bjørn, P. A., Heuch, P. A., and Elston, D. A. 2005. Population dynamics of salmon lice *Lepeeophtheirus salmonis* on Atlantic salmon and sea trout. Marine Ecology Progress Series, 290: 263–275.

Thorstad, E. B., Økland, F., Finstad, B., Sivertsgård, R., Bjørn, P. A., and McKinley, R. S. 2004. Migration speeds and orientation of Atlantic salmon and sea trout post-smolts in a Norwegian fjord system. Environmental Biology of Fishes, 71: 305–311.

Tingley, G. A., Ives, M. J., and Russell, I. C. 1997. The occurrence of lice on sea trout (*Salmo trutta* L.) captured in the sea off the East Anglian coast of England. ICES Journal of Marine Science, 54: 1120–1128.

Tuff Carlsen, K., Berg, O. K., Finstad, B., and Heggberget, T. G. 2004. Diel periodicity and environmental influence on the smolt migration of Arctic charr, *Salvelinus alpinus*, Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta*, in northern Norway. Environmental Biology of Fishes, 70: 403–413.

Tully, O., and Nolan, D. T. 2002. A review of the population biology and host-parasite interactions of the sea louse *Lepeophtheirus salmonis* (Copepoda: Caligidae). Parasitology, 124: 165–182.

Tully, O., and Whelan, K. F. 1993. Production of nauplii of *Lepeophtheirus salmonis* (Krøyer) (Copepoda: Caligidae) from farmed and wild salmon and its relation to the infestation of wild sea trout (*Salmo trutta* L.) off the west coast of Ireland in 1991. Fisheries Research, 17: 187–200.

Wagner, G. N., McKinley, R. S., Bjørn, P. A., and Finstad, B. 2003. Physiological impact of sea lice on the swimming performance of Atlantic salmon. Journal of Fish Biology, 62: 1000–1009.

Wagner, G., McKinley, R. S., Bjørn, P. A., and Finstad, B. 2004. Short-term freshwater exposure benefits sea lice-infected Atlantic salmon. Journal of Fish Biology, 64: 1593–1604.

doi:10.1093/icesjms/fsl029

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