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INTRODUCTION

The Strategic Framework for Scottish Aquaculture (Scottish Executive, 2003) aims to adopt best practice in management and control of disease and pathogens. This report fulfils an undertaking of the Strategic Framework, and reviews research and field data in Scotland and abroad on relative louse infection levels on wild salmon smolts and sea trout and the proximity of fish farms to river estuaries. Sea lice infestation of farmed salmonids and their effects on wild salmonids have been the subject of a great deal of research and monitoring in recent years (see Boxaspen, 2005). The aquaculture industry has received much criticism regarding control of sea lice and links to falling wild salmonid numbers. However, the science required to examine any link between fish farming and wild fish populations is complex and difficult, and it is only through the review of work from different groups and over long time periods that trends and links become clear. This review aims to illuminate some of the main findings from a large amount of research carried out in the major salmon farming countries of the Northern hemisphere.

Sea Lice Biology

The biology of sea lice was comprehensively reviewed by Pike & Wadsworth (1999). Sea lice are caligid copepod parasites of fish. In Scotland, both *Lepeophtheirus salmonis* (Krøyer, 1837) and *Caligus elongatus* (Nordmann, 1832) species are found on farmed Atlantic salmon *Salmo salar* L. Of these, *L. salmonis* causes the most serious problems, with overall abundance of *C. elongatus* lower than *L. salmonis*, and significant inverse relationships between the two species (Revie *et al.*, 2002a). In this review, where the louse species is not explicitly stated, the text refers to *L. salmonis*.

Sea louse eggs hatch to release free-living planktonic stages. These nauplii develop into infective copepodids that use chemosensory mechanisms to locate their hosts (Invarsdóttir *et al.*, 2002). Following settlement on a host, lice proceed through chalimus larvae and pre-adult stages to adults (Johnson & Albright, 1991; Piasecki, 1996; Schram, 1993).

L. salmonis has circumpolar distribution. Study of the population genetics of *L. salmonis* found that there was a lack of genetic differentiation between populations, indicating few barriers to gene flow and essentially random mating (see Boxaspen, in press, for review). This might be surprising if lice were thought to complete their entire life cycle in restricted areas such as bays, lochs or fjords. In fact, lice survive on Atlantic salmon throughout the winter and in the feeding grounds, where random mating is possible (see below).

Host Preference

In aquarium experiments, sea trout were not found to be more susceptible to louse infection than Atlantic salmon (Bjørn & Finstad, 1998). Although Dawson *et al.* (1997) found that the attachment and survival of chalimus stages was lower on salmon, and salmon had lower lice abundance than sea trout, no significant differences were found in the attachment and survival of *L. salmonis* to sea trout or salmon in aquarium experiments (Bricknell, Fisheries Research Services, personal communication). The intensities of lice on sea trout and char are also similar (Bjørn *et al.*, 2001), although it was found that large trout and char tended to have lower infestation than smaller fish (Bjørn & Finstad, 2002). In aquarium experiments analysing the susceptibility of sea run and freshwater brown trout (*Salmo trutta*), although the survival and development of lice was similar on both groups, sea trout had lower abundance and intensity of infection (Glover *et al.*, 2001). It was not determined whether variations in the degree of louse attachment or loss caused these differences and it was postulated that natural selection for resistant fish may have influenced the lice levels in sea trout. In another study, some differences in susceptibility of sea trout populations were found (Glover *et al.*, 2003), with a population that may historically have been exposed to more frequent and intensive lice infestation having significantly lower lice abundance, density and rate of development. In this experiment, louse density was proportional to fish length and weight.

No significant differences in lice infestation were found between different farm stocks of Atlantic salmon, but the density on one wild salmon stock was significantly lower than on another wild and a farm strain (Glover *et al.*, 2004).

It is clear that *L. salmonis* prefers salmonids to other fish and that within a species, differences in lice levels between stocks may be found. However, no clear differences in susceptibility have been demonstrated between species and the degree of variation within a species may exceed that between species. Thus at present it appears that sea trout are not innately more susceptible to sea lice than Atlantic salmon.

Difficulties Studying Lice on Wild Fish

In the case of wild fish studies, there are many environmental variables that may influence lice infestation data (see MacKinnon, 1998). These include season, temperature, current, salinity and water quality in addition to host factors such as age, size, stock and immunocompetence and pathogen influences such as strain, viability, fecundity and pathogenicity. The number and variability of these factors creates extreme difficulty in comparing different studies. Many of these factors also impact on wild populations of fish and their stock sizes, making it extremely difficult to determine primary causes for decreases in wild fish stocks.

It can be problematical to compare studies if different variables have been measured in each case. Experimental variation also complicates the use of results from different studies. Catch methods is one obvious source of this variation (see Jacobsen & Gaard, 1997). In most studies on lice, accepted definitions of intensity, abundance and prevalence have been used (Margolis *et al.*, 1982), so that although use of abundance data may be difficult (as stated below) and care is required when using data from separate reports, at least it is technically possible to compare data from different studies.

There may of course be many reasons for a decline in levels of natural populations such as sea trout and the ultimate cause of mortality in wild fish is very difficult to define. It is also difficult to prove a cause/effect relationship between the infection of wild fish and mortality, with extrapolation from aquarium experiments to wild populations being extremely problematical (McVicar, 2004). It can be difficult to draw conclusions from complex patterns of wild fish population decline (McVicar, 1997; 2004), but periodic consideration of available evidence may advance knowledge on the subject.

Overdispersion, or aggregation, is a situation where only a few hosts in a population have a large parasite burden and the majority of the host population have few or no parasites. In experiments, *L. salmonis* chalimus stages were overdispersed in intensity on sea trout post-smolts, but this overdispersion decreased at later stages of lice (Bjørn & Finstad, 1998). In areas where salmon farms are present, infections of sea trout and char were overdispersed (Bjørn *et al.*, 2001). In a review of data sets, Murray (2002) concluded that sea lice were overdispersed on sea trout from a range of marine environments and that the degree of overdispersal was highest in coastal areas, near salmon farms.

The overdispersion of lice on hosts creates serious difficulties in interpreting data, particularly that from wild fish. In an over-dispersed distribution, most of the lice are on a few fish with very high loads. This makes obtaining a representative sample difficult, making estimates of mean abundance and intensity unreliable. The population effects of lice loads may be insensitive to the mean intensity; impact may instead depend on the proportions of host that have lice loads above a certain intensity. This proportion cannot be calculated from mean loads, unless the distribution of loads is also known and this is not often reported. The existence of over-dispersion may be inferred if variance in intensity of infestation exceeds the mean.

As is the case for any disease condition, lice infestation is extremely difficult to study in wild fish. To draw conclusions or reveal trends, the results of many different studies must be reviewed.

Effects of Lice Infestation on Salmonids

L. salmonis induces systemic stress responses in the skin and gills of infected salmonids (Tully & Nolan, 2002), with intensity of infection correlated with stress indicators such as plasma cortisol (Bowers *et al.*, 2000; Bjørn *et al.*, 2001). The susceptibility of fish to lice and the consequences of infestation are also affected by host factors of species, life cycle stage and health status, including stress, nutrition and immunocompetence (MacKinnon, 1998).

Dawson *et al.* (1997) found that the general pattern of skin damage caused by lice was the same on salmon and sea trout. McVicar *et al.* (1993) found that sea trout captured in north western Scotland in early summer had cranial lesions and fin erosion consistent with sea lice damage, but MacKenzie *et al.* (1998) only found dorsal fin damage, associated with chalimus infection. Other pathological changes were seen in these fish, notably in the internal organs, but could not be correlated with disease, illustrating the difficulty inherent in examining the health status or causes of mortality in wild fish.

Dawson (1998) investigated the physical and physiological impact of lice on wild sea trout in Ireland. Dorsal fin erosion was the only physical damage reported, and was found in fish with higher lice intensities, but no skin damage was found in fish bearing pre-adult or adult parasites. Fin erosion has also been associated with chalimus stage infection of sea trout in Scotland (McVicar *et al.*, 1993) but there was no clear relation between numbers of lice and degree of damage. No correlation was found between physiological parameters and lice numbers and physiological differences between groups of fish could not be unequivocally attributed to lice infection.

Schram *et al.* (1998) found a prevalence of 100% *L. salmonis* on adult sea trout off southern Norway by late autumn, with median intensity at a maximum of 8 lice per fish. There was little damage to the fish caused by the lice and no correlation between infestation and condition factor of the fish, indicating that these levels of lice did not cause serious damage to the trout.

The swimming performance of infected salmon in seawater is significantly lower than that of uninfected fish or infected fish in freshwater, suggesting that return to freshwater may relieve osmotic stress and reduce the energy requirement of infected fish (Glover *et al.*, 2004). Although *L. salmonis* may remain on salmon up to 6 days after return to freshwater, most lice are lost in the first 48 hours (McLean *et al.*, 1990). Therefore data on lice burdens on fish captured in freshwater or in estuarine areas where fish may have entered freshwater then returned to seawater must be treated with care.

Louse infection of sea trout and landlocked salmon was found to be correlated with changed behaviour and premature return to freshwater (Bjørn *et al.*, 2001; Carr & Whoriskey, 2004; Finstad & Birkeland, 1997; Grimnes *et al.*, 1998). Infested landlocked salmon that returned to freshwater had significant damage (Carr & Whoriskey, 2004). The consequences of this early return of infested sea trout was studied by Birkeland (1996). Post-smolts carried more lice than older sea trout and these lice were mainly copepodids and chalimus, in contrast to the older lice carried by older fish. 41% of the post-smolts that entered freshwater later returned to sea and had recovered from the louse infestation. A review of these and further results from Norway (see Heuch *et al.*, 2005) indicates that premature return was not unusual during the late 1990s.

Despite the many practical considerations in using or analysing results from multiple sources, an accumulation of information from many different studies may reveal general patterns, trends or correlations. A review of information regarding sea lice damage to salmonids reveals that severe lice infestation causes physiological disturbance and physical harm to salmon and sea trout. There is currently no evidence that either species suffers more damage than the other. The levels of lice infestation that may be harmful have been studied in some detail (see below).

Harmful Levels of Lice

Harmful levels of *L. salmonis* were estimated by Bjørn & Finstad (1997) and Finstad *et al.* (2000) who found that development of lice to pre-adult and adult stages was accompanied by a sudden increase in the osmoregulatory imbalance of sea trout and salmon smolts and mortality of sea trout smolts. It was estimated that lice levels above 90 larvae or 50 pre-adult or adult lice could result in the death of 60g sea trout smolts (Bjørn & Finstad, 1997) and over 30 chalimus larvae may kill 40g salmon smolts when the lice develop to pre-adults (Finstad *et al.*, 2000). No mechanical damage was found to sea trout post smolts until pre-adult stages of lice developed and this damage was more frequent and severe on moribund fish (Bjørn & Finstad, 1998). McVicar *et al.* (1993) found that wild post-smolt sea trout may be infected with more than 100 chalimus larvae without suffering physiological impairment, in contrast to smolts, which appear to suffer once lice levels reach 90 larvae per 60g smolt (Bjørn & Finstad, 1997). Jacobsen & Gaard (1997) found a mean abundance of 30 *L. salmonis* on salmon in feeding grounds north of the Faroe islands. This level of infestation did not appear to cause damage to the fish. The variance:mean ratio of infection on wild sea trout smolts studied by Bjørn *et al.* (2001) was thought to indicate mortality of the fish with the highest infections. Salmon smolts may not survive infection of more than 11 lice (see Heuch *et al*., 2005). This louse level caused mortality in aquarium experiments (Finstad *et al.*, 2000) and smolts collected from the wild (Holst *et al*., 2003). In addition, no wild smolts with more than 10 lice were found (Holst *et al*., 2003), which may indicate mortality of those that are more heavily infected.

On the east coast of Canada, wild fish examined for lice infestation had less damage than expected from the observed lice burdens, and this was taken as evidence that infection had occurred recently, potentially with larvae from nearby farms (Carr & Whoriskey, 2004).

The general conclusion is that development of lice from larvae to pre-adult and adult stages increases the harmful effects of the lice. Smolting fish appear more susceptible to damage than post-smolts. Therefore, infection of wild salmonids as they head out to sea is likely to have a greater effect than infection of mature returning fish.

Baseline Lice Levels in Areas Without Farms

As many authors have already pointed out, it is desirable to have baseline data on lice levels in different areas from the era prior to fish farming. As this information is not available, surveys have been undertaken in regions without farming activity.

On wild salmonids, both *L. salmonis* and *C. elongatus* have been recorded (Boxaspen, 2005 table 1). In Scotland, *C. elongatus* was rarely found on sea trout, with most lice on this species being *L. salmonis* (McVicar *et al.*, 1993, MacKenzie *et al.*, 1998).

In wild Atlantic salmon, Todd *et al.* (2000) found lice prevalence of 82-100%, with a greater abundance on older fish, indicating persistent infection in the open ocean and not just in lochs.

Studies of wild sea trout by McVicar *et al.* (1993) and MacKenzie *et al.* (1998) found up to 30% of trout infected with lice. Great variation in infection intensity was found by MacKenzie *et al.* (1998), and as noted above, small numbers of fish infected with many lice can skew the figures of lice abundance for an area. *L. salmonis* chalimus stages were overdispersed in intensity on experimentally infected sea trout post-smolts, but this overdispersion decreased at later stages of lice (Bjørn & Finstad, 1998). Conversely, overdispersion was found as infection progressed in wild sea trout and char (Bjørn *et al.*, 2001).

MacKenzie *et al.* (1998), Bjørn *et al.* (2001), Bjørn & Finstad (2002) and Rikardsen (2004) all found that in areas remote from farms, the lice showed a progression of developmental stages with time, with low infestations in winter and spring, dominated by adult lice whereas higher infestations in autumn contained a high proportion of chalimus larvae.

Tingley *et al.* (2001) studied louse levels on sea trout caught in the North Sea off England, an area remote from salmonid farming. 96% prevalence and a mean abundance of 4 lice per fish, with 0-13 lice per fish, including chalimus stages, indicating that transmission had occurred in seawater. Seasonal effects on infestation were greater than annual, weight, condition factor, age, sex or sea time. Lice were overdispersed, but to a lesser degree than in areas where salmonids are farmed, and *Caligus elongatus* infestations were more dynamic than *L. salmonis*. Salmon returning to Ireland were also infested, with a prevalence of over 94%, including some juvenile lice (Copley *et al.*, 2005).

In a region of Norway remote from salmonid farms, Schram *et al.* (1998) found that the prevalence of *L. salmonis* on sea trout reached 100% in autumn, from 20-35% in March and April, but the prevalence and intensity of *C. elongatus* was lower. Similar levels of lice were found in another region by Mo & Heuch (1998). Prevalence and intensity increased in Spring but decreased from May to July. In sampling areas further north in Norway, lower prevalence levels were found on both sea trout and char and in one year the sampling area distant from farms had more lice than the area with farms (Bjørn & Finstad, 2002). Lower intensity in this study may be related to temperature effects or the density of fish farming in the region. Schram *et al.* (1998) suggested that the patterns of prevalence, infestation and aggregation indicated that lice did not cause serious damage to the trout. Mo & Heuch (1998) did not find any prematurely returning sea trout. In contrast to the findings of Butler *et al.* (2001), adult stages of lice dominated the Norwegian samples.

The findings of Todd *et al.* (2000), Tingley *et al.* (2001) and Copley *et al.* (2005) provide evidence that salmonids maintain a population of lice throughout the year. This is supported by the finding of all life stages of lice in salmon feeding grounds. Jacobsen & Gaard (1997) sampled salmon north of the Faroes. Prevalence of *L. salmonis* was 99.2% and *C. elongatus* 5.5%. The abundance and density of lice, especially chalimus and pre-adult stages, was higher on escapee 1 seawinter fish than on wild fish, but on 2 seawinter fish, infestation was similar. The presence of all stages of lice on fish in open-oceans indicates that infestation occurs here as well as in coastal locations. Although infestation in winter is low and infection success reduced, lice do survive through winter months and can reproduce (Boxaspen 2005; Boxaspen & Naess, 2000; Heuch *et al.*, 2002).

In sea trout too, a population of lice is maintained throughout the year and in regions remote from farms. Seasonal patterns of infestation of sea trout in northern Norway were observed, similar to those found by Schram *et al.* (1998), with prevalence reaching over 80% in autumn (Rikardsen, 2004). These data indicated the sea trout maintain a population of sea lice through feeding in seawater even in winter.

Once the data from the studies cited above are reviewed, it can be seen that *L. salmonis* prevalence of over 95% is usual in areas without salmon farms. Populations of lice are maintained throughout the year and during time spent in feeding grounds remote from aquaculture. The seasonality of prevalence and intensity levels requires that care is taken when interpreting data from only a few time points or samples taken at only certain seasons. Nevertheless, the combined data from these studies provide some indication of base line lice levels in the absence of salmon farms.

Release of Lice from Farms

Lice and other parasitic copepods pose a serious problem for fish farming (see Johnson *et al.*, 2004). These infestations, and the potential risks to wild fish, have been 'one of the most intensively reviewed topics in aquatic biology' (McVicar, 2004).

As louse infection pressure is a product of the number of fish in the system and the number of lice per fish (Heuch & Mo, 2001), it is undeniable that heavy infestation of lice in fish farms increases the infection pressure in the area, with numbers of farmed salmonids in Norway estimated to be over 10 times greater than the number of wild hosts (Heuch *et al.*, 2005). The link between louse infection of wild fish and proximity of fish farms has received intense scrutiny and infections of wild fish are an important indicator for the success of lice control strategies (Heuch *et al.*, 2005). Scottish farms have higher infection levels than those in Norway, possibly related to differences in temperature, environment, or treatments (Heuch *et al.*, 2003; Revie *et al.*, 2003b). Data from Scottish Atlantic salmon farms showed inter-annual variation in lice levels, but no association between lice levels and geographical region, stock type or coastal exposure (Revie *et al.*, 2002b), although high current speed was associated with lower lice burdens (Revie *et al.*, 2003a). Treatments led to pronounced cycles of infestation and were significantly correlated with numbers of chalimus, although not with numbers of mobile stages (Revie *et al.*, 2002b; 2003a).

McKibben & Hay (2002; 2004a) sampled copepodids close to a river mouth over a period of 2 years. The greatest peak density of louse copepodids ever recorded was found close to the river mouth. Copepodids were only found at the river mouth when the nearby salmon farm was in its second year of production and contained gravid female lice. This relationship was also found in samples from another river (McKibben & Hay, 2004a; b) and can be related to higher *L. salmonis* numbers on farms in the second year of production (Treasurer *et al.*, 2004). This was also seen in Canada (Anon, 2005). This contrasts with *C. elongatus*, which has greater abundance in the first year (McKenzie *et al.*, 2004). Butler (2002) estimated that 78-99% of louse eggs produced in 2000 originated from farmed fish, with escaped farm salmon contributing most of the remainder. Larval lice can be dispersed at least 4.6km from farms (McKibben & Hay, 2004a). Northcott *et al.* (2001) also noted high densities of lice copepodids at the tide margin.

The link between lice on farms and copepodids found in open water and near river mouths was also noted by Penston *et al.* (2004). Pulses of infection were found, with highest densities near the shore. Although louse copepodids do aggregate near step salinity gradients (Heuch, 1995), the high densities found near river mouths by Penston *et al.* (2004) were probably as a result of wind-driven transport of the larvae. Pulses of lice abundance were also seen by Marshall (2003).

Dispersal of larvae seems to be largely governed by physical processes such as wind and tide, with a net transport towards the shore on the west coast with a prevailing westerly wind, resulting in high densities at estuaries (see Tully & Nolan, 2002; McKibben & Hay, 2002; 2004a). A three-dimensional particle advection model showed extremely high variability in lice distribution in Norwegian fjords, with spreading of 0-100km in only a few days (Asplin *et al.*, 2004), due to faster coastal currents and slower larval development in the lower temperatures found there compared to Scotland. This agrees with Murray's (2002) description of patchy distribution, albeit not accounting for patchiness in time. Bends or narrowing of the fjord resulted in convergence and/or retention of the lice. Analysis of field data from Scotland, Norway, England and Wales and Ireland confirms a degree of overdispersion, shown by variance exceeding the mean. This aggregated distribution is not explained solely by pulses of infection, but requires infection to be patchy in space as well as time, possibly in infection hot spots (Murray, 2002).

More data has been collected in Ireland. Tully & Whelan (1993) estimated that 95% of nauplius I *L. salmonis* in midwest Ireland were of farmed origin. Costelloe *et al.* (1996) studied planktonic larvae and their dispersion. As expected, the highest density of lice was found inside salmon cages, with the density outside the cage less than 10% of this, and decreasing with distance from the cage such that density 1km from the cage was 90% less than that 10 m from the cage, and few larvae were found more than 2 km from the farm.

A study conducted by Tully (1989) used a sentinel cage of salmon smolts among other cages and examined the prevalence and intensity of both *L. salmonis* and *C. elongatus*. The data indicated that most of the infestation originated from the farmed fish. Sentinel cages were also used by Costelloe *et al.* (1995), where salmon smolts were placed at varying distances from a salmon farm. The cage near the river mouth had the highest density of lice, as might be expected given the results shown by McKibben & Hay (2002; 2004a). However, lice from the farm did not appear to contribute greatly to larval density in the inner harbour, as may be expected from the hydrography of the area. Population structures of lice varied with time and between cages, with the lice settling in pulses rather than continuously.

The production of nauplii on the farms studied by Tully & Whelan (1993) was relatively constant between March and July. Seasonal variation was also seen by Costelloe *et al.* (1998a; b) in plankton samples from three bays in Ireland. The highest density of larvae was found during spring and then numbers decreased. Larvae were only consistently found close to a salmon farm. Peak larvae numbers in Killary harbour could be linked to peaks in the nearby farm.

Jackson *et al.* (1997) analysed data on lice infestations from *Salmo salar* and *Oncorhynchus mykiss* farms on the west coast of Ireland. *O. mykiss* tended to have lower infestations but differences in infestation were found between sites that were attributed to husbandry practices. Fallow periods of 14 days were long enough to break the cycle of lice infection, with minimum practical lice levels being those resulting from re-infestation from wild sources. Longer fallow periods are usually preferred, given the length of the louse life cycle, but need not be too onerous, as fallowing for over 7 weeks had no advantage over fallow periods of 5-7 weeks (Treasurer *et al.*, 2004). Fallowing has no effect on *C. elongatus* infestation, which is less host-specific and may have many alternative hosts (Revie *et al.*, 2002a).

Oncorhynchus species have also been found to carry more lice in areas associated with salmon farms (Morton *et al.*, 2004) with a drop in lice levels when farms are fallowed (Morton *et al.* , 2005). It has been suggested that the presence of farms increases infection pressure in this area of British Columbia by over 70 times (Krkošek *et al.*, 2005). However, this conclusion was based on limited data and another study found similar levels of prevalence and intensity of lice (*L. salmonis* and *Caligus clemensi*) on Pacific salmon in areas with and without farms (Beamish *et al.*, 2005). Pacific species have lower infestation levels than Atlantic salmon in the same region (British Columbia, 2004). On farms in Japan, these infestations do not create serious problems as the farm cycle is shorter than a year (Nagasawa, 2004).

Despite the problems inherent in using results and data from different studies, it is clear that farms with high numbers of sea lice increase the louse infection pressure in the vicinity. Nevertheless, the relationship between numbers of lice on the farm and numbers of infective larvae in the surrounding area is not straightforward. The release of larvae from farms is not continuous but occurs in pulses, leading to larval distribution that is patchy in time. Dispersal processes such as wind, current and freshwater input result in larval spreading that is not uniform, but is patchy in space. Although there are difficulties in interpreting some data on larval production and dispersal, it is apparent that husbandry practices on farms have a significant effect on lice infestation, with fallow periods of 6 weeks effectively breaking cycles of *L. salmonis* infection.

Lice Levels on Wild Fish in the Vicinity of Salmon Farms

In Scotland, wild sea trout were found infested with lice and bearing damage caused by the lice. Heaviest lice infection was found in samples in the west and northwest, areas where most salmon farming takes place, but even so, fish sampled in late summer and autumn did not have lice or lesions and fish captured on the east of Scotland also had high lice numbers but no evidence of physical damage. Thus, no clear link was found between lice intensity and proximity of salmon farms (McVicar *et al*., 1993; MacKenzie *et al.*, 1998), with the latter study finding that although fish on farms could be heavily infected in April and May, wild sea trout nearby had only scarce or no infections. This might be explained by pulses of lice abundance. These pulses were also seen by Marshall (2003) although the relationship between lice on wild salmonids and on a nearby farm was only weak. Although there was evidence of progression through stages of the louse life cycle, chalimus stages dominated on the wild salmonids sampled by Marshall (2003). The farm in this study was unusual in having a three-year cycle with a one year fallow instead of the two year production cycle common in Scotland.

Data collected by Sharp *et al.* (1994) revealed that a high intensity of chalimus stages was associated with a greater intensity of lice. Considerable variation in louse population structure was found in this study, even from within the same loch. The degree of overdispersion was highest with highest median intensity, and the lower overdispersion found in sea trout confined in sea cages indicates that this may be a result of uneven distribution of lice larvae in the loch and/or the trout frequently entering and leaving freshwater (Sharp *et al.*, 1994). This pattern of distribution fits well with the model of patchy distribution described by Murray (2002).

Valuable data have been collected by the Association of West Coast Fisheries Trusts (AWCFT) in Scotland (Butler *et al.*, 2001; Butler, 2002). Only *L. salmonis* were found on the trout, supporting similar findings by Sharp *et al.* (1994). Over the period 1994-2000, the highest lice burden and pooled abundance data showed a general increase although there was a wide variation both geographically and inter-annually. All sites sampled were less than 26 km from active salmon farms and localized lice epizootics were found, with a variation in site and year that correlated with farm cycles. A higher louse abundance on wild fish was found when nearby farms were in the second year of production. This might be expected from McKibben & Hay's findings of more lice larvae in plankton samples when nearby farms are in the second year of the production cycle (McKibben & Hay, 2004a; b).

Where mixed year classes were found in the samples collected by the AWCFT (Butler *et al.*, 2001; Butler, 2002), aggregate lice abundance was higher, with post smolt infections dominated by chalimus stages, whereas pre-adults dominated the infections of older fish. Heavy chalimus infections were associated with damage to the dorsal fins. The proportion of fish carrying a louse burden greater than the potentially lethal number of 30 (Grimnes & Jakobsen, 1996) varied, from 13.5% to 39.5% in different years. In the Dundonnell river, despite 48-99% of sea trout carrying more than 30 lice, only 4 moribund fish were found (Butler, 2001). This contrasts with the findings in Ireland where many infected and moribund fish were seen (Tully *et al.*, 1993a). Since 2000, monitoring by the AWCFT has continued in Scotland, with correlation between higher lice abundance when nearby farms are in the second year of production, but an overall decrease in lice abundance in the period 2000-2004.

The effects of sea lice on wild salmonids has received a great deal of attention since heavy lice infestations were said to coincide with collapses of sea trout stocks in Ireland where mortality at sea had risen to 95% since 1989 Tully *et al.* (1993b). Angling catches of Scottish sea trout, particularly in the northwest, also show a decline from the 1950s to the 1990s (McVicar *et al.*, 1993). The same situation was found in Ireland (Tully & Whelan, 1993), and also England and Wales, an area without extensive marine aquaculture (McVicar, 2004).

As discussed previously, it is notoriously difficult to determine the direct cause of any decline in wild fish stocks. McArdle *et al.* (1993) found *Aeromonas salmonicida* infection in 3 of 6 catchments where sea trout were returning prematurely. They suggest that diseases other than sea lice may have had a role in the falling sea trout numbers in Ireland. Nevertheless, the hypothesis that heavy sea lice infestation was leading to the premature return of wild sea trout and causing a drastic reduction in these stocks has received a great deal of attention and has been the subject of much research.

Tully *et al.* (1993b) sampled sea trout on their return to freshwater at 36 sites in northwest Ireland. The prevalence and intensity of lice ranged from 21-92% and 2-53%, respectively. The population structure of the lice varied, being over 80% copepodid and chalimus at 15 sites, but less than 20% at 7 sites. The population structure may reflect the length of time spent at sea or the length of time since infection.

Louse infestation on sea trout in 42 estuaries in Ireland over 5 years was examined by Tully *et al.* (1999). Sea trout post smolts showed high retention in the bay in which they migrate, but the life cycle of the louse was thought to be too long to account for horizontal transmission between sea trout in a bay. Although infestation data was highly variable, it could be shown that spatial variation was greater than temporal, with significant differences in infestation between regions, bays within a region and estuaries within a bay. Infestation was significantly higher in areas where infected farms were also present, with the presence of farms being correlated with 3.5 times greater mean abundance of lice on sea trout. However, the production of larvae in one region did not influence infestation data in other regions.

Gargan *et al.* (1993; 2003) also found a relationship between lice on sea trout and distance from salmon aquaculture. Sea trout sampled at rivers that were varying distances from fish farms had higher maximum and median numbers of lice and a higher proportion of chalimus stages at sites close to farms. Infestations were below median level at all sites distant from farms. Highest mean lice numbers were found less than 20 km from farms and chalimus stages, indicating recent transmission, dominated infections less than 30 km from farms. Physiological and osmoregulatory problems were expected when louse levels exceeded 0.7 larvae per g fish weight, and many more sea trout in bays with salmon farms had lice above this harmful level than did sea trout in bays with no farms. Therefore it was concluded that the risk of carrying damaging lice infestations is related to the distance from farms and sea trout survival may be inversely related to lice levels.

However, some samples obtained close to farms had relatively low infestation (Gargan *et al.*, 1993). This may be influenced by the length of time the fish had been at sea, but will also be affected by the release of infective lice larvae from farms.

It was reported that the production of nauplii from farms in April was correlated with the number of lice infesting wild sea trout 3 weeks later. However, although the production of nauplii on farms was relatively constant between March and July, the transmission to sea trout appeared to be restricted to late April and May (Tully & Whelan, 1993).

Tully *et al.* (1999) found that sea trout infestation with lice differs significantly in space and time and proposed that these differences were related to pulses of lice production on farms and that cross-infection with lice was possible between farms located closer than 10km to each other. As physical processes of wind and tide have significant effects on louse larval transport, these should also be carefully considered when examining the probability of cross-infection or larval transport from farms to estuaries.

In Norway too, there is a correlation between sea trout infestation and proximity to farms. Higher louse abundance was found on sea trout, salmon and char in areas of Norway where there was salmon farming (Bjørn *et al.*, 2001; Bjørn & Finstad, 2002; Grimnes *et al.*, 1998). Younger lice predominated in sea trout and char infections at all time points sampled at sites associated with fish farming, (Bjørn *et al.*, 2001; Bjørn & Finstad, 2002). In northern Norway, epidemics were seen in sea trout and char in an area where there was fish farming activity (Bjørn & Finstad, 2002). However, in northern Norway, the link between high louse infestation in farms and epizootics on wild fish is not as clear as in the southwest of the country (Heuch *et al.*, 2005).

Boxaspen (1997) found lice settlement on salmon in Norway was inversely related to distance from an infested farm. Interestingly, lice counts and temperature data from the preceding winter could be used to predict lice numbers in the following summer. This is confirmed by findings that initial spring production determines lice loads in that year (Murray, 2002; Revie *et al.*, 2003a).

The levels of lice production from farms that constitute a threat to wild salmonids are not known and neither is it clear whether lice regulate sea trout populations. Nevertheless, it is considered highly likely that salmon farming has caused louse epizootics in southwest Norway (Heuch *et al.*, 2005). Heuch *et al.* (2005) provide an expert review of the routes by which wild salmonids may be infected by sea and point out the influences of environmental and ecological factors that influence the infection dynamics and may give rise to variable findings on the timing of infection in different regions. Data on the harmful effects of lice on sea trout indicate that the mean intensity should be restricted to less than 11 lice per fish to avoid harm. This level is unlikely to be feasible in Norway at current levels of farming and lice infestation on farms (Heuch *et al.*, 2005). It is recommended that low levels of lice must be maintained throughout the year, and not just during spring and summer, to protect wild salmonids (Heuch *et al.*, 2005). Although further work is required to understand the population dynamics, and the resulting infection pressure of sea lice better (Stien *et al.*, 2005), high levels of lice on farms do pose a hazard for wild fish. The outcomes of the Hardangerfjord project in Norway (DIPnet, 2005) could provide valuable information on the interactions of lice between wild and farmed fish in a fjord system.

The lack of damage caused by lice infestation of wild salmon on the East coast of Canada did not suggest that lice were causing a decline in wild populations there (Carr & Whoriskey, 2004). The lice levels on farmed and wild fish here both increased until 2000, when new lice treatments became available for the farms.

In European waters, sea trout smolts remain close to the shore when they first enter seawater, staying in inner fjord systems whereas salmon smolts move throughout the fjord, into the open ocean (Dieperink *et al.*, 2001; Finstad *et al.*, 2005). If there is a high density of infective lice in this area, it will provide an optimum source of infection for smolts. Indeed, Northcott et al., (2001) and McKibben & Hay (2004b) found that sea trout are infected with lice soon after going to sea.

Smolts may return to freshwater to remove lice burdens and/or hyperosmotic stress. It is thought that the premature return of infested sea trout is probably common in areas where there is salmon farming (Heuch *et al.*, 2005). In Scotland, more premature returns of sea trout were recorded in the second year of the farm's production cycle (Northcott *et al.*, 2001; McKibben & Hay, 2002). The second year of production is also the time when the highest numbers of infective lice larvae are found near the shore.

Although there is no conclusive proof that heavy lice burdens and premature return of sea trout smolts are causal factors in the decline of wild populations, where control measures are feasible, steps taken to reduce the incidence of infective lice larvae in areas where wild salmon and sea trout smolts enter seawater will reduce the potential for harmful infestation of the wild fish.

Regulatory Control of Sea Lice

All major salmon farming countries in the Northern hemisphere now have active control of sea lice, with varying types of formal regulation of lice control. Integrated sea lice management in Scotland is promoted through Area Management Agreements and the salmon farming industry association Code of Practice, whose objectives include synchronous fallowing in each management area, and aim to have zero ovigerous sea lice, especially during wild smolt migration periods (Scottish Executive, 2004). The timing of treatment is very important, and may be informed by models such as those of Revie *et al.* (2005) and Stien *et al.* (2005).

Sea lice monitoring was introduced in Irish fin-fish farms in 1994 with particular attention paid to lice levels during the smolt migration period in spring (Jackson *et al.*, 1997). Single bay management was also introduced (Copley *et al.*, 2001), with efficacy of treatment varying with treatment type and life cycle stages, and some bays having more successful lice control than others.

The Norwegian National Action Plan set threshold lice levels for periods when wild smolts are migrating. In Canada, action is required once infestation reaches 3 mobile lice, whatever the time of year (Anon, 2005). Since the inception of the action plan in Norway, levels of lice on wild salmon smolts in Sognefjord have dropped, but no reduction was found on sea trout smolts in middle and north Norway or south west fjords. The mean number of lice per fish in farms has reduced. However, as the total number of farmed fish may have increased in the same period, it is not clear if this reduction in average lice per fish has led to a reduction in the total number of lice or not (Heuch *et al.*, 2005). Estimating the probability of success of this action plan is hampered by lack of knowledge on the levels of lice that will cause harm to wild populations, nevertheless it is considered that the high number of farmed fish in production is likely to result in lice levels that pose a risk to wild populations (Heuch *et al.,* 2005).

CONCLUSIONS

Infestation of salmonids with lice is a natural phenomenon that occurs at all phases in the seawater stage of their lifecycle. Studying the infection of wild fish and their interaction with farmed populations is extremely difficult. However, a large body of knowledge has been gained from many studies on lice on salmonids, especially since the 1990s, in several countries.

Reviewing the results of many studies allows some conclusions to be reached. Heavy lice infestation is damaging and can be ultimately fatal for any salmonid. In salmon farms, heavy infestation leads to the release of extremely high numbers of infective larvae. This release seems to occur in pulses rather than continuously, and the dispersal of the larvae can be complex, influenced by wind, tide and hydrology of the area. Where these processes bring infective lice in contact with wild salmonids, higher than background levels of infestation can occur. This may prompt return to freshwater or perhaps even mortality. The levels of lice that are likely to cause detrimental effects depend on the size and species of the fish concerned.

Significant measures to reduce lice burdens in farms are in place in all salmon farming countries of the northern hemisphere. These, coupled with development of effective treatments, have been successful in reducing lice counts on farmed fish in recent years.

Lice levels on wild fish are the ultimate measure of the success or otherwise of sea lice control measures. These are difficult to determine and must be considered in the light of knowledge of the harmful levels of lice for that species and stage of the life cycle. The most appropriate controls for farms will depend on factors such as the local environment, the ecology of wild fish in the vicinity, and the regulation of medicines, and therefore it continues to be difficult to draw conclusions based on findings from one region or country and to extrapolate these to other areas. Nevertheless, it is apparent that measures to reduce lice levels on farms to extremely low levels are required in order to prevent harm to wild fish in the surrounding area.

REFERENCES

Anon. 2005. Sea Lice Management Strategy. Government of British Columbia. http://www.agf.gov.bc.ca/fisheries/health/sealice_MS.htm

Asplin, L., Boxaspen, K. and Sandvik, A.D. 2004. Modelled distribution of salmon lice in a Norwegian fjord. ICES CM 2004/P:11, 12pp.

Beamish, R.J., Neville, C.M., Sweeting, R.M. and Ambers, N. 2005. Sea lice on adult Pacific salmon in the coastal waters of Central British Columbia, Canada. *Fisheries Research*, **76**, 198-208.

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

Birkeland, K. and Jakobsen, P.J. 1997. Salmon lice, *Lepeophtheirus salmonis*, infestation as a causal agent of premature return to rivers and estuaries by sea trout, *Salmo trutta*, juveniles. *Environmental Biology of Fishes*, **49**, 129-137.

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. & Finstad, B. (1998) The development of salmon lice (*Lepeophtheirus salmonis*) on artificially infected post smolts of sea trout (*Salmo trutta*). 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. 2001. Salmon lice infection of wild sea trout and Arctic char in marine and freshwaters: the effects of salmon farms. *Aquaculture Research*, **32**, 947-962.

Bowers, J., Mustafa, A., Speare, D., Conboy, G., Brimacombe, M., Sims, D. and Burka, J. 2000. The physiological response of Atlantic salmon, *Salmo salar* L., to a single experimental challenge with sea lice, *Lepeophtheirus salmonis*. *Journal of Fish Diseases*, **23**, 165-172.

Boxaspen, K. 1997. Geographical and temporal variation in abundance of salmon lice (*Lepeophtheirus salmonis*) on salmon (*Salmo salar*). *ICES Journal of Marine Science*, **54**, 1144-1147.

Boxaspen, K. 2005. Sea lice biology and genetics. ICES Journal of Marine Science. In press.

Boxaspen, K. and Naess, T. 2000. Development of eggs and the planktonic stages of salmon lice (*Lepeophtheirus salmonis*) at low temperatures. *Contributions to Zoology*, **69**, 51-55.

British Columbia. 2004. Review of Sea Lice Management Oct. 1, 2003 thru Sept. 30, 2004.

Butler, J.R.A. 2001. Dundonnell river sea lice monitoring: summary of results, 1997-2001. Wester Ross Fisheries Trust, Gairloch, Scotland, 9pp.

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 salmon farms. *Pest Management Science*, **58**, 595-608.

Butler, J.R.A., Marshall, S., Watt, J., Kettlewhite, A., Bull, C., Bilsby, M., Bilsby, H., Ribbens, J., Sinclair, C.A., Stoddart, R.C. and Crompton, D.W.T. 2001. Patterns of sea lice infestations on Scottish west coast sea trout: survey results, 1997-2000. Association of West Coast Fisheries Trusts, 22pp.

Carr, J. and Whoriskey, F. 2004. Sea lice infestation rates on wild and escaped farmed Atlantic salmon (*Salmo salar* L.) entering the Magaguadavic river, New Brunswick. *Aquaculture Research*, **35**, 723-729.

Copley, L., McCarney, P., Jackson, D., Hassett, D., Kennedy, S. and Nulty, C. 2001. The occurrence of sea lice (*Lepeophtheirus salmonis* Krøyer) on farmed salmon in Ireland (1995 to 2000). *Marine Resource Series No 17*, 17pp.

Copley, L., Tierney, T.D., Kane, F., Naughton, O., Kennedy, S., O'Donohoe, P., Jackson, D. and McGrath, D. 2005. Sea lice, *Lepeophtheirus salmonis* and *Caligus elongatus*, levels on salmon returning to the west coast of Ireland, 2003. *Journal of the Marine Biological Association of the UK*, **85**, 87-92.

Costelloe, J., Costelloe, M. and Roche, N. 1995. Variation in sea lice infestation on Atlantic salmon smolts in Killary Harbour, West Coast of Ireland. *Aquaculture International*, **3**, 379-393.

Costelloe, M., Costelloe, J. and Roche, N. 1996. Planktonic dispersion of larval salmon-lice *Lepeophtheirus salmonis*, associated with cultured salmon, *Salmo salar*, in Western Ireland. *Journal of the Marine Biological Association of the UK*, **76**, 141-149.

Costelloe, M., Costelloe, J., Coghlan, N., O'Donohoe, G. and O'Connor, B. 1998a. Distribution of the larval stages of *Lepeophtheirus salmonis* in three bays on the west coast of Ireland. *ICES Journal of Marine Science*, **55**, 181-187.

Costelloe, M., Costelloe, J., O'Donohoe, G., Coghlan, N.J., Oonk, M. and Van Der Heijden, Y. 1998b. Planktonic distribution of sea lice larvae *Lepeophtheirus salmonis*, in Killary harbour, west coast of Ireland. *Journal of the Marine Biological Association of the UK*, **78**, 853-874.

Dawson, L.H.J. 1998. The physiological effects of salmon lice (*Lepeophtheirus salmonis*) infections on returning post-smolt sea trout (*Salmo trutta*) in western Ireland, 1996. *ICES Journal of Marine Science*, **55**, 193-200.

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. I*CES Journal of Marine Science*, **54**, 1129-1139.

Dieperink, C, Pedersen, S. and Pedersen, M.I. 2001. Estuarine predation on radiotagged wild and domesticated sea trout (*Salmo trutta* L.) smolts. *Ecology of Freshwater Fish*, **10**, 177-183.

DIPnet (2005) Newsletter 6: The Hardangerfjord salmon lice project. http://www.dipnet.info/newsletters/index.asp

Dixon, B.A., Shinn, A.P. and Sommerville, C. 2004. Genetic characterization of populations of the ectoparasitic caligid, *Lepeophtheirus salmonis* (Krøyer, 1837) using randomly amplified polymorphic DNA. *Aquaculture Research*, **35**, 730-741.

Finstad, B. and Birkeland, K. 1997. Salmon lice infestations in orally treated and non-treated sea-trout. ICES CM 1997/M:4. Report of the 1996 workshop on interactions between salmon lice and salmonids.

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.) post-smolts. *Aquaculture Research*, **31**, 795-803.

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

Gargan, P., Whelan, K.F. and Tully, O. 1993. Infestation of Sea Trout (*Salmo trutta* L.) by sea lice (*Lepeophtheirus salmonis* (Krøyer)) in systems close to and distant from salmon farms in Ireland. ICES CM 1993/M56, 16pp.

Gargan, P., Tully, O. and Poole, W.R. 2003. Relationship between sea lice infestation, sea lice production and sea trout survival in Ireland, 1992-2001. In: Mills, D. (Ed.) Salmon on the Edge, Blackwell, Oxford, 119-135.

Glover, K.A., Nilsen, F., Skaala, Ø., Taggart, J.B. and Teale, A.J. 2001. Differences in susceptibility to sea lice infection between a sea run and a freshwater resident population of brown trout. *Journal of Fish Biology*, **59**, 1512-1519.

Glover, K.A., Skaala, Ø., Nilsen, F., Olsen, R., Teale, A.J. and Taggart, J.B. 2003. Differing susceptibility of anadromous brown trout (*Salmo trutta* L.) populations to salmon louse (*Lepeophtheirus salmonis* (Krøyer, 1837)) infection. *ICES Journal of Marine Science*, **60**, 1139-1148.

Glover, K.A., Hamre, L.A., Skaala, Ø. and Nilsen, F. 2004. A comparison of sea louse (*Lepeophtheirus salmonis*) infection levels in farmed and wild Atlantic salmon (*Salmo salar* L.) stocks. *Aquaculture*, **232**, 41-52.

Grimnes, A. and Jakobsen, P.J. 1996. The physiological effects of salmon lice (*Lepeophtheirus salmonis* Krøyer) infection on post smolt of Atlantic salmon (*Salmo salar*). *Journal of Fish Biology*, **48**, 1179-1194.

Grimnes, A., Finstad, B., Bjørn, P.A., Tovslid, B.M. and Lund, R. 1998. Registrations of salmon lice on Atlantic salmon, sea trout and Arctic charr. *NINA Oppdragsmelding*, **525**, 1-33.
Heuch, P.A. 1995. Experimental evidence for aggregation of salmon louse copepodids (*Lepeophtheirus salmonis*) in step salinity gradients. *Journal of the Marine Biological Association UK*, **75**, 927-939.

Heuch, P.A., Knutsen, J.A., Knutsen, H. and Schram, T. 2002. Salinity and temperature effects on sea lice over-wintering on sea trout *(Salmo trutta)* in coastal areas of the Skagerrak. *Journal of the Marine Biological Association of the UK*, **82**, 887–892.

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., Revie, C.W. and Gettinby, G. 2003. A comparison of epidemiological patterns of salmon lice, *Lepeophtheirus salmonis*, infections on farmed Atlantic salmon, *Salmo salar* L., in Norway and Scotland. *Journal of Fish Diseases*, **26**, 5390551.

Heuch, P.A., Bjørn, P.A., Finstad, B., Holst, J.C., Asplin, L. and Nilsen, F. 2005. A review of the Norwegian 'National action plan against salmon lice on salmonids': the effect on wild salmonids. *Aquaculture*, **246**, 79-92.

Holst, J.C., Jacobsen, P., Nilsen, F., Holm, M., Asplin, L. and Aure, J. 2003. Mortality of seaward-migrating post-smolts of Atlantic salmon due to salmon lice infection in Norwegian salmon stocks. In: Mills, D. (Ed.) Salmon on the Edge, Blackwell, Oxford, 136-137.

Ingvarsdóttir, Birkett, M.A., Duce, I., Genna, R.L., Mordue, W., Pickett, J.A., Wadhams, L.J. and Mordue (Luntz), A.J. 2002. Semiochemical strategies for sea louse control: host location cues. *Pest Management Science*, **58**, 537-545.

Jacobsen, J.A. and Gaard, E. 1997. Open-ocean infestation by salmon lice (*Lepeophtheirus salmonis*): comparison of wild and escaped farmed Atlantic salmon (*Salmo salar* L.). *ICES Journal of Marine Science*, **54**, 1113-1119.

Jackson, D., Deady, S., Leahy, Y. and Hassett, D. 1997. Variations in parasitic caligid infestations on farmed salmonids and implications for their management. *ICES Journal of Marine Science*, **54**, 1104-1112.

Johnson, S.C. and Albright, L.J. 1991. The developmental stages of *Lepeophtheirus salmonis* (Krøyer, 1837) (Copepoda: Caligidae). *Canadian Journal of Zoology*, **69**, 929-950.

Johnson, S.C., Treasurer, J.W., Bravo, S., Nagasawa, K. and Kabata, Z. 2004. A review of the impact of parasitic copepods on marine aquaculture. *Zoological Studies*, **43**, 229-243.

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 B*, **272**, 689-696.

McArdle, J.F., Dooley-Martyn, C., Geoghegan, F., McKiernan, F. and Rodger, H. 1993. Furunculosis as a possible factor in the decline of sea trout in the West of Ireland. *Fisheries Research*, **17**, 201-207.

McKenzie, E., Gettinby, G., McCart, K. and Revie, C.W. 2004. Time-series models of sea lice *Caligus elongatus* (Nordmann) abundance on Atlantic salmon *Salmo salar* L. in Loch Sunart, Scotland. *Aquaculture Research*, **35**, 764-772.

MacKenzie, K., Longshaw, M., Begg, G.S. and McVicar, A.H. 1998. Sea lice (Copepoda: Caligidae) on wild sea trout (*Salmo trutta* L.) in Scotland. *ICES Journal of Marine Science*, **55**, 151-162.

McKibben, M.A. and Hay, D.W. 2002. Planktonic distribution of sea lice *Lepeophtheirus salmonis* larvae in inter-tidal plankton samples in Loch Shieldaig, Western Scotland in relation to local salmon farm production cycles. ICES CM 2002/T:06. 13pp.

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

McKibben, M.A. and Hay, D.W. 2004b. Larval sea lice densities and sea lice levels on post-smolt sea trout in western Scotland, 2002-2003. FRS Report 04/04, 21pp.

MacKinnon, B.M. 1998. Host factors important in sea lice infections. *ICES Journal of Marine Science*, **55**, 188-192.

McLean, P.H., Smith, G.W. and Wilson, M.J. 1990. Residence time of the sea louse, *Lepeophtheirus salmonis* K., on Atlantic salmon, *Salmo salar* L., after immersion in fresh water. *Journal of Fish Biology*, **37**, 311-314.

McVicar, A. H. (1997) Disease and parasite implications of the coexistence of wild and cultured Atlantic salmon populations. ICES Journal of Marine Science 54: 1093-1103.

McVicar, A.H. 2004. Management actions in relation to the controversy about salmon lice infections in fish farms as a hazard to wild salmonid populations. *Aquaculture Research*, **35**, 751-758.

McVicar, A.H., Sharp, L.A., Walker, A.F. and Pike, A.W. 1993. Diseases of wild sea trout in Scotland in relation to fish population decline. *Fisheries Research*, **17**, 175-185.

Margolis, L., Esch, G.W., Holmes, J.C., Kuris, A.M. and Schad, G.A. 1982. The use of ecological terms in parasitology (Report of an ad hoc committee of the American Society of Parasitologists). *Journal of Parasitology*, **68**, 131-133.

Marshall, S. 2003. The incidence of sea lice infestations on wild sea trout compared to farmed salmon. *Bulletin of the European Association of Fish Pathologists*, **23**, 72-79.

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.

Morton, A., Routledge, R., Peet, C. and Ladwig, A. 2004. Sea lice (*Lepeophtheirus salmonis*) infection rates on juvenile pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon in the nearshore marine environment of British Columbia, Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, **61**, 147-157.

Morton, A., Routledge, R. and Williams, R. 2005. Temporal Patterns of Sea Louse Infestation on Wild Pacific Salmon in Relation to the Fallowing of Atlantic Salmon Farms. *North American Journal of Fisheries Management*, **25**, 811–821.

Murray, A.G. 2002. Using observed load distributions with a simple model to analyse the epidemiology of sea lice (*Lepeophtheirus salmonis*) on sea trout (*Salmo trutta*). *Pest Management Science*, **58**, 585-594.

Nagasawa, K. 2004. Sea lice, *Lepeophtheirus salmonis* and *Caligus orientalis* (Copepoda: Caligidae), of wild and farmed fish in sea and brackish waters of Japan and adjacent regions: a review. *Zoological Studies*, **43**, 173-178.

Northcott, S.J., Bresnan, E.M., McKibben, M.A. and Walker, A.F. 2001. The primary location of infection of sea trout, *Salmo trutta* L., post-smolts by *Lepeophtheirus salmonis* (Krøyer), in a Scottish sea loch. FRS Report. 20pp.

O'Shea, B., Mordue (Luntz), A.J. and Bricknell, I.R. 2003. Host preferences of the salmon louse, *Lepeophtheirus salmonis*. 6th International conference on the biology and control of sealice, St Andrews, Canada, 1-4 July, 2003.

Penston, M.J., McKibben, M.A., Hay, D.W. and Gillibrand, P.A. 2004. Observations on open-water densities of sea lice larvae in Loch Shieldaig, Western Scotland. *Aquaculture Research*, **35**, 793-805.

Piasecki, W. 1996. The developmental stages of *Caligus elongatus* von Nordmann, 1832 (Copepoda: Caligidae). *Canadian Journal of Zoology*, **74**, 1459-1478.

Pike, A.W. and Wadsworth, S.L. 1999. Sea lice on salmonids: Their biology and control. *Advances in Parasitology*, **44**, 234-337.

Revie, C.W., Gettinby, G., Treasurer, J.W. and Rae, G.H. 2002a. The epidemiology of the sea lice, *Caligus elongatus* Nordmann, in marine aquaculture of Atlantic salmon, *Salmo salar* L., in Scotland. *Journal of Fish Diseases*, **25**, 391-399.

Revie, C.W., Gettinby, G., Treasurer, J.W., Rae, G.H. and Clark, N. 2002b. Temporal, environmental and management factors influencing the epidemiological patterns of sea lice (*Lepeophtheirus salmonis*) infestations on farmed Atlantic salmon (*Salmo salar*) in Scotland. *Pest Management Science*, **58**, 576-584.

Revie, C.W., Gettinby, G., Treasurer, J.W. and Wallace, C. 2003a. Identifying epidemiological factors affecting sea lice *Lepeophtheirus salmonis* abundance on Scottish salmon farms using general linear models. *Diseases of Aquatic Organisms*, **57**, 85-95.

Revie, C.W., Heuch, P.A. and Gettinby, G. 2003b. Epidemiological patterns of *Lepeophtheirus salmonis* infections: a country-level comparison on salmon farms in Norway and Scotland. 6th International conference on the biology and control of sealice, St Andrews, Canada, 1-4 July, 2003.

Revie, C.W., Robbins, C., Gettinby, G., Kelly, L. and Treasurer, J.W. 2005. A mathematical model of the growth of sea lice, *Lepeophtheirus salmonis*, populations on farmed Atlantic salmon, *Salmo salar* L., in Scotland and its use in the assessment of treatment strategies. *Journal of Fish Diseases*, **28**, 603-613.

Rikardsen, A.H. 2004. Seasonal occurrence of sea lice *Lepeophtheirus salmonis* on sea trout in two north Norwegian fjords. *Journal of Fish Biology*, **65**, 711-722.

Schram, T.A. 1993. Supplemetary descriptions of the developmental stages of *Lepeophtheirus salmonis* (Krøyer, 1837) (Copepoda: Caligidae) In: Pathogens of wild and farmed fish: sea lice. Eds. G. Boxshall & D. Defaye. Ellis Horwood, London, pp. 30-47.

Schram, T.A., Knutsen, J.A., Heuch, P.A. and Mo, T.A. 1998. Seasonal occurrence of *Lepeophtheirus salmonis* and *Caligus elongatus* on sea trout *Salmo trutta* off southern Norway. *ICES Journal of Marine Science*, **55**, 163-75.

Scottish Executive. 2003. Strategic Framework for Scottish Aquaculture. The Stationery Office, Edinburgh, 70pp.

Scottish Executive. 2004. Tripartite Working Group. http://www.scotland.gov.uk/Topics/Fisheries/Fish-Shellfish/18677/14221

Sharp, L., Pike, A.W. and McVicar, A.H. 1994. Parameters of infection and morphometric analysis of sea lice from sea trout (*Salmo trutta* L.) in Scottish waters. In: Parasitic Diseases of Fish. Eds. A.W. Pike and J.W. Lewis. Dyfed, Samara Publishing Ltd. 151-170.

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

Todd, C.D., Walker, A.M., Hoyle, J.E., Northcott, S.J., Walker, A.F and Ritchie, M.G. 2000. Infestations of wild adult Atlantic salmon (*Salmo salar* L.) by the ectoparasitic copepod sea louse *Lepeophtheirus salmonis* Krøyer: prevalence, intensity and the spatial distribution of males and females on the host fish. *Hydrobiologia*, **429**, 181-196.

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.

Treasurer, J., Revie, C.W. and Gettinby, G. 2004. Examination of extensive data sets reveal patterns of sea lice abundance in Scotland. Fish Farmer March/April 2004: 12-13.

Tully, O. 1989. The succession of generations and growth of the caligid copepods *Caligus elongatus* and *Lepeophtheirus salmonis* parasitising farmed Atlantic salmon smolts (*Salmo salar* L.). *Journal of the Marine Biological Association of the UK*, **69**, 279-287.

Tully, O., Poole, W.R., Whelan, K.F. and Merigoux, S. 1993a. Parameteres and possible causes of epizootics of *Lepeophtheirus salmonis* (Krøyer) infesting sea trout (*Salmo trutta* L.) off the west coast of Ireland. *In* Pathogens of wild and farmed fish: Sea Lice. Eds. Boxshall, G. A., Defaye, D. Ellis Horwood, Chichester. Pp. 202-213.

Tully, O., Molloy, S., Gargan, P., O'Maoileidigh, Whelan, K.F. and Poole, R. 1993b. Infestation of sea trout (*Salmo trutta* L.) by the salmon louse (*Lepeophtheirus salmonis* Krøyer) in Ireland during 1993. ICES CM 93/M14, 11pp.

Tully, O., Gargan, P., Poole, W.R. and Whelan, K.F. 1999. Spatial and temporal variation in the infestation of sea trout (*Salmo trutta* L.) by the caligid copepod *Lepeophtheirus salmonis* (Krøyer) in relation to sources of infection in Ireland. *Parasitology*, **119**, 41-51.

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**, S165-S182.

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.

Tully, O., Gargan, P., Poole, W.R. and Whelan, K.F. 1999. Spatial and temporal variations in the infestation of sea trout (*Salmo trutta* L.) by the caligid copepod *Lepeophtheirus salmonis* (Krøyer) in relation to sources of infection in Ireland. *Parasitology*, **119**, 41-51.

Wagner, G.N., 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.