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August 2010

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Background

For the past four decades the Atlantic Salmon Trust has been involved in the funding and sponsorship of practical research programmes tackling the problems facing populations of wild Atlantic salmon (*Salmo salar* L) and sea trout (*Salmo trutta* L). The Trust's work centres on improving our knowledge of these fish, their habitats and their complex and fascinating life histories. To date the Trust's direct support for research has focused on research awards, which mainly took the form of seed funding for a broad range of fisheries related projects. This approach proved very successful and laid the foundation for many key advances in fisheries management over the years. In addition the Trust was to the fore in funding marine related research and is one of the main funders of the current multinational and interdisciplinary SALSEA Merge Programme (www.salmonatsea.com). Building on its involvement with this programme, the Trust has now decided to embark on the establishment of an AST Fellowship Scheme which will, on a partnership basis, seek to fund key and pressing areas of research. In conjunction with this initiative the Trust will compile a series of reviews to summarise the current state of scientific knowledge in a number of key areas. The AST will develop a set of policy statements outlining the Trust's views on key management areas. It will also identify where additional work is urgently required and how AST's research goals link with these management objectives.

Introduction

This is the first such scientific review and seeks to summarise the current state of scientific knowledge in relation to the impacts of the salmon louse, *Lepeophtheirus salmonis* on wild salmonids. Sea lice are the most significant parasitic pathogen in salmon farming in Europe and are estimated to cost the world industry €300m a year. Over the past two decades there has been increasing evidence that lice from salmon farms can increase the abundance of sea lice in adjacent bays and estuaries and impact adversely on wild migratory salmonid stocks. Research work is ongoing on the issue and in recent years has focused mainly on quantifying the risk of transmission from farmed sources to the wild migratory hosts. This review summarises what is known regarding the biology of the salmon louse, how the impacts were first discovered, what advances have been made in identifying and quantifying the key parameters involved and the development of sea lice transmission and distribution models, which may well hold the key to future management strategies.

Biology of the Sea Louse

Sea lice (Copepoda, Caligidae) are natural parasites of both salmon and sea trout. Two genera of lice, *Lepeophtheirus* and *Caligus,* are commonly found on wild salmonids and in more recent times have caused the greatest economic impact on salmon farms. *Lepeophtheirus salmonis* is the dominant species found on farmed and wild salmonids in Northern Europe. Costello (2006) reviewed in detail the known ecology of the salmon louse.

Life cycle of the salmon louse

The female salmon louse carries her eggs in a pair of egg sacs extruding from her abdomen. The number of eggs per sea louse varies with time of year, louse size, louse age and host species. Based on earlier studies it is generally assumed that sea lice on farmed salmon carry an average of 500 ova while those on wild salmon carry 1000 ova (Costello, 2006) but more recent research would indicate that these estimates are conservative (Heuch, Nordhagen and Schram, 2000).

The eggs hatch in sequence and the female louse can produce six to eleven broods over her lifetime. Following release, the eggs float in the surface plankton and hatch into a first larval stage called the nauplius. There is no evidence for a sea louse resting stage over-wintering in near shore habitats. Some of the eggs produced by *L. salmonis* in near shore environments may develop into larvae that infect three spined sticklebacks (*Gasterosteus aculeatus*); large numbers of chalimus larvae and a very few pre-adults have recently been found on this species (Jones *et al*., 2006), but there is no evidence that *L. salmonis* can complete its lifecycle on sticklebacks (Losos, 2008) or on any species other than a salmonid host (Revie *et al*., 2009)

As can be seen from Figure 1, the louse has two initial larval stages, termed nauplii, both of which are non-feeding and planktonic. Depending on ambient temperatures the nauplii moult after 5 to 15 days into infective free-living copepodids. Once they have located a host they attach by means of their antenna. The copepodid moults into the chalimus stage which is attached to the host by a special frontal filament. There are four successive sessile chalimus stages that feed on the host skin around their point of attachment. In *L. salmonis* there are two further immature pre-adult stages during which the lice move freely over the host skin to feed. These mobile stages attach to the host with a chalimus-like filament when moulting. The life span of the louse is difficult to measure but adults can over-winter on wild salmon.

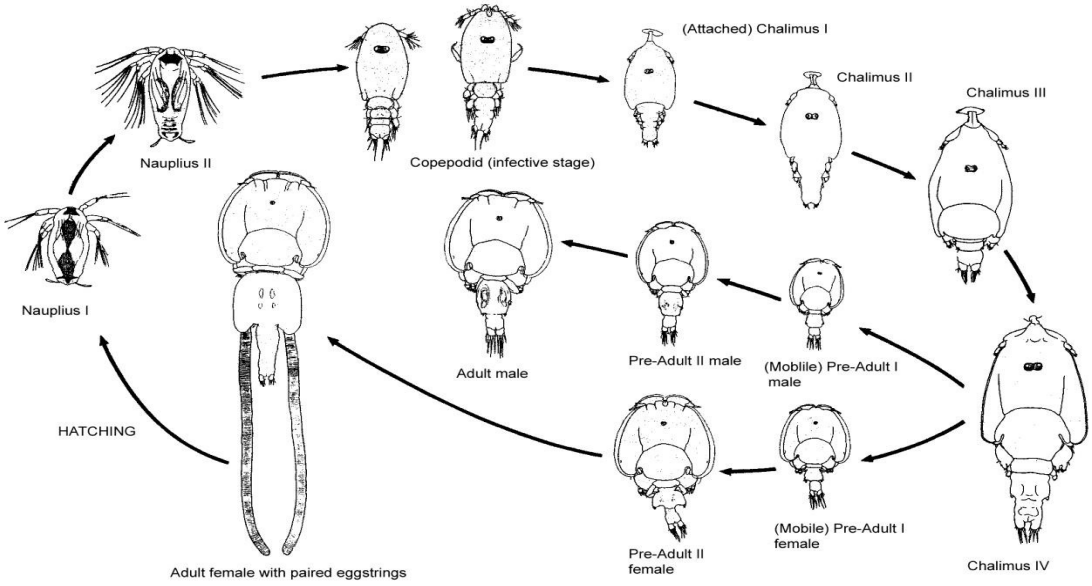

Figure 1. The stages in the life-cycle of the sea louse *Lepeophtheirus salmonis*. The Nauplius I & II and copepodid are free-living planktonic stages.

Feeding methods and impacts on the host

Sea lice use rasping mouth parts to graze the host and remove mucus, skin and underlying tissue. They can occur anywhere on the body but often congregate on the head of the host and behind the fins. They grip their host with their second pair of antennae and maxillipeds (a foot-like mouth appendage). Mobile lice are designed so that water flow presses them to the host's surface over which they swim by jet propulsion. Impacts on the host's skin include epithelium loss, bleeding, increased mucus discharge, altered mucus biochemistry, tissue necrosis and consequent loss of physical and microbial protective function. Host fish have reduced appetite, growth and food conversion efficiency, and the stress and wounds expose fish to secondary infections. Changes to the host's blood include anaemia, reduced lymphocytes, ion imbalance and elevated cortisol. These changes indicate a stressed and weakened host, with reduced osmoregulatory and respiratory ability and impaired immunocompetence.

Sea louse growth is strongly dependent on temperature. Typically sea lice live longer and grow larger at colder temperatures. Larger females produce more eggs. Consequently over-wintering females are larger and release more eggs in spring than summer females. Because spring eggs are also larger, spring larvae have greater food reserves and as a consequence can spend longer in the plankton searching for a suitable host.

However, increased average sea temperatures, whether due to annual variation or as predicted by climate change scenarios for future decades, are likely to increase louse abundance on wild and farmed fish as a result of shorter generation times. In addition, they are likely to affect the geographical distribution of sea lice and their wild hosts, potentially bringing new sea louse species into contact with wild and farmed fish. Another possibility is that locally increased maximum temperatures may stress sea lice and /or their hosts.

Distribution of louse larvae

Epizootics or heavy infestations of sea lice on wild fish consist almost entirely of early chalimus stages, indicating that the fish simultaneously encounter high concentrations of the infective planktonic copepodids. Plankton sampling in sea inlets in the mid-west of Ireland revealed that louse larvae, especially infective copepodids, are most abundant in shallow estuarine areas, ideal locations to intercept migratory salmonids (Costelloe, 1995). These studies revealed a rapid decrease in sea louse nauplius concentrations away from fish farms, but no such trends for copepodids. Sampling programmes in two Scottish sea lochs repeatedly produced the highest concentrations of copepodids in shallow water near the estuary mouths (Penston *et al*., 2004; McKibben and Hay, 2004). Indeed, the highest concentrations of these larvae were caught with hand-nets by researchers wading along the shore, rather than from nets towed by boats. It thus seems that *L. salmonis* larvae not only move vertically in the water column, but are transported horizontally towards shallow waters, where salmonids are more abundant.

Larval dispersal

L. salmonis do not find their hosts only in estuaries. The presence of chalimi on wild salmon in the offshore Atlantic and Pacific oceans indicates they receive low levels of *L. salmonis* infestation when away from the coast. The typical development of infestations on farmed salmon indicate that many of the lice larvae are available to re-infest their parent's hosts, and plankton sampling has shown that not all copepodids disperse away from the cages. Salmonids typically feed at the surface in farm cages and also come near the surface to feed in the wild. Thus vertical movement of sea louse larvae or their hosts could increase opportunity for parasite / host contact.

A transmission model for *L. salmonis*

Costello (2006) proposed a transmission model to explain how sea louse larvae of *L. salmonis* are concentrated into shallow coastal and estuarine waters. Nauplii swim upwards during the day but do not actively swim downwards. They are thus likely to concentrate in surface waters. During the day onshore winds, generated by thermo-convection from the warmer land, drive surface waters containing the sea lice towards the shore and towards estuaries. Where fresh water lies on the surface, sea louse larvae can congregate along the halocline, or freshwater-saltwater interface. Tidal currents increase in estuaries as the tidal volume is forced into a narrow channel. This increase in current velocity ensures that lice entrained in the water column cover greater distances and thus increases the likelihood of copepodids being close to a potential host, although host attachment might be more difficult in stronger currents.

These options for the transmission model have recently been field tested (Armundrud and Murray, 2009; Gillibrand and Willis, 2007) and the results are discussed in a later section of this review.

Locating their hosts

Sea lice are very effective at locating potential hosts. Laboratory work has shown that hosts may be attracted to what appears to be a crustacean prey item in the plankton, but upon approach, the louse may dodge predation and attach to the host (Connors *et al*., 2009). The lice may detect

movement of the host by mechano-sensors from approximately 26 mm distance (Heuch *et al*., 2006), but they may also be attracted by water-borne host odours, as well as contact chemosensors once attached to the host (Mordue Luntz *et al*., 2006; Fields *et al*., 2007; Pino-Marambio *et al*., 2007; Mordue & Birkett, 2009). Both copepodid and adult lice can discriminate their preferred host species using both odour and taste, and pre-adult female lice attract males using pheromones (Mordue & Birkett, 2009).

History of the problem in Ireland

Infestations of juvenile sea lice were first recorded on sea trout along the west coast of Ireland in the spring of 1989. Irish west coast sea trout are relatively slow growing and long lived in comparison with salmon, and their life cycle is far more complex. Sea trout remain in fresh water for two to four years before migrating to sea as smolts and they will return three or more times to spawn in fresh water. In general Irish sea trout populations flourish where growth rates in fresh water are poor, where survival in fresh water is difficult and where there is easy access to the sea. As a result under natural conditions survival fluctuates widely, both in freshwater and at sea and alternating periods of dearth and abundance may appear in consecutive years. Because of the marginal existence of the species, there was evidence throughout the 1970s and the 1980s of a slow decline in stock abundance. This was largely attributable to illegal netting and a range of environmental problems such as field drainage, stream drainage and maintenance, fertilisation of the hillsides, afforestation and, in the late 1980s, hillside erosion due to overgrazing by sheep (Whelan, 1992).

Whelan (1991, 1992 and 1993) describes a more serious and dramatic decline, which appeared along the western sea board of Ireland in 1986 and had, by 1989, resulted in a collapse of sea trout stocks in many mid western fisheries (Whelan and Poole 1996). Unfortunately, little sea trout research was taking place at this time but information is available on the sequence of events which took place during the May / June period of 1989. In mid May, within weeks of having migrated to sea, large numbers of post- smolts appeared in the estuaries of the Delphi and Erriff systems in Counties Galway and Mayo. These fish were in some distress and on closer examination it was found that the trout were infested with high densities of sea lice larvae. Damage to the skin and fins was very severe on many of the fish examined. Samples of the fish were immediately dispatched to the national fish pathologist for examination. His results confirmed that the fish had severe infestations of juvenile salmon lice *L. salmonis*.

The fish were in poor physical condition, the post-smolts had grown little while at sea and moribund and dead fish were commonly observed in a number of estuaries. Sea trout populations plummeted following this event. Trap census data from the Burrishoole System in County Mayo indicates that between 1971 and 1988 the average percentage survival of sea trout from smolts to finnock ranged between 11.4% and 32.4%. In 1988 it fell from the previous recorded minimum to 8.5%, and in 1989 to 1.5% (Poole *et al*., 1996).

Although sea lice infestation was clearly implicated in these events, there was no systematic research under way to identify the source of the lice. In 1991 the Irish Government established a Sea Trout Working Group to examine the available evidence and to establish the likely causes of the lice infestation and the sea trout stock collapse. Over the next three years a great deal of detailed scientific research was carried out on the observed phenomena and the likely causes. Much of this research work was funded by the Sea Trout Action Group (STAG), a voluntary sea trout conservation group, established in the late 1980s, following concerns regarding rapidly declining sea trout stocks in the mid west of Ireland.

The results of this work were published in the reports of the Sea Trout Working Group (Anon 1992, 1993, 1994 and 1995) and subsequently in the peer-reviewed scientific literature by Tully, 1992; Tully, Poole and Whelan, 1993; Tully, Poole, Whelan, and Merigoux, 1993b; Tully and Whelan, 1993; Whelan, 1993; Whelan and Poole, 1996; Poole *et al*., 1996 and Tully, Gargan, Poole and Whelan, 1999).

Infestation parameters and source of infestation

Tully, Poole and Whelan (1993) established a set of infestation parameters, including prevalence, intensity and abundance, for *L. salmonis* infesting sea trout for a number of locations along the west coast of Ireland in 1990 and 1991. Based on these parameters, sites were classified into two groups in 1990 and three groups in 1991. Median infestation intensity in these groups was 11.6 and 77 lice per fish in 1990 and 9.5, 29.5 and 55 per fish in 1991. Fish were mainly parasitised by chalimus stages of the parasite which attached preferentially to the fins.

The age structure of the louse population on individual fish was generally restricted to a few life stages, proximal to each other in the life cycle, indicating that transmission of the parasite to individual fish was restricted in time. The age structure was different at heavily infested sites compared to moderately and lightly infested sites in both 1990 and 1991. At other sites, and particularly for those where post-smolts (up to one year at sea after smoltification) displayed a normal return pattern to fresh water, pre-adult and adult lice predominated. At heavily infested sites the louse population was composed entirely of copepodid and chalimus stages. At heavily infested sites in 1991 pre-adults and some adult lice were recorded but again chalimus stages predominated. In 1990, when samples were taken over a 3 - 4 month period, there was a complete lack of maturation of the louse population on fish at heavily infested sites and in both years the total number of lice per fish had the highest positive correlation with the number of chalimus stages, indicating that heaviest infestations were invariably due to these stages. These observations imply that either all the lice died before reaching a pre-adult stage, that all hosts infested with large numbers of chalimus stages died before these stages matured, or that different groups of fish were being sampled on each sampling date.

Tully, Poole, Whelan and Merigoux (1993) examined infestation parameters for *L. salmonis* infesting sea trout post-smolts during May 1992 at 14 locations along the west coast of Ireland. In the 1992 study, prevalence ranged from 14.3% to 100%, and mean intensity from 7 to 124.7. The maximum number of lice recorded on an individual fish was 325. As in 1990 and 1991 the louse population infesting these fish was immature and dominated by chalimus stages. These were attached predominantly to the fins of the fish. No copepodids were recorded, indicating that infestations had not occurred for a number of days prior to the fish being captured. Most pre-adult and adult lice were recorded at sites where infestations were comparatively light.

The morphological impact of lice on host sea trout was significant. The rays of the fins were exposed and extensive grazing marks and skin erosion were evident on the dorsal side of the fish. Mortality of infested fish was directly observed each year.

Overall it was shown that in Ireland infestation of sea trout by *L. salmonis* developed to epizootic proportions in 2 – 3 weeks. Because the copepodid is obliged to find a host within days of moulting from nauplius II stage (Fig1), its transmission must therefore occur close to the location where the nauplii are produced.

Research was also carried out at this time to estimate the relative proportions of sea lice from wild and farmed salmonids. Tully and Whelan (1993) estimated the number and fecundity of ovigerous *L. salmonis* infesting wild and farmed salmon and daily production from these fish of nauplius I larvae between March and July 1991. They concluded that farmed salmon contributed 95% of the total production of Nauplius I in the mid west region. They also concluded that on a finer scale this production may vary in different embayments and was determined primarily by the size of the farmed stock held at each location. This production may also vary between years, both due to changes in the size of the farmed and wild stocks and because of the effects of changing temperatures over a twelve month period, on the rate of development and the number of generations the parasite produces. Although the production of nauplii remained relatively constant between March and July, transmission to sea trout was apparently restricted in time to April and May. Tully and Whelan concluded that temporally varying susceptibility to infestation may therefore have a role in determining the level of infestation that develops.

Over the period of the study the population structure of lice-infested sea trout caught during the first half of May was dominated by chalimus stages, suggesting that the fish were infested during mid April. A correlation between larval production in mid April and subsequent parasitic intensity

of sea lice on sea trout at the beginning of May would be expected if transmission to sea trout is related to local production from farmed sources. Events during 1992 provided evidence for a correlation as changes in larval production led to predicted changes in the level of infestation of sea trout. In Killary Harbour, production of *L. salmonis* nauplii from farmed sources decreased to zero in April 1992 due to fallowing of the bay. Infestation of sea trout in Killary during May 1992 fell to 25% of the 1991 level. Production of nauplii from farmed salmon in Clew Bay rose from zero in 1991 to very significant levels in April 1992, while infestation of sea trout caught in Clew Bay increased from a mean of 12.6 lice per fish in 1991 to 55 in 1992. Similar close correlations between the presence or absence of salmon farming in a given bay and the survival rates of sea trout were reported by Whelan and Poole in 1996.

Tully (1993) also showed that temperatures in these west coast bays had increased throughout the 1980s and estimated the impact of these changes on sea lice production. Temperature data from the Irish North West coast for the years 1980 – 1991 showed that the potential number of *L. salmonis* generations per year approached 7 in 1989 - 1991, compared with 5.5 in 1985 – 1988. Winter generation times in 1980 -1981 varied between 95 and 125 days and were approximately 3 weeks shorter in each winter between 1989 and 1991 compared with earlier years.

The similar levels of infestation apparent in different estuaries sharing the same embayment in 1991 also suggested that the sea area into which the fish migrates is important in determining the level of infestation that will develop, and supported the view that transmission rates may be correlated with densities of, or encounter rates with, copepodids.

Characterisation of the Problem

Tully and Whelan (1993) concluded that the collapse of the sea trout populations in the mid-west of Ireland was characterised by: the premature return of smolts and kelts to estuaries and fresh water, a proportion of which subsequently died; heavy infestations of a proportion of smolts and kelts by juvenile sea lice; the presence of emaciated fish, at least in 1989; a significant reduction in the spawning stock. It was also apparent that the bulk of the production of nauplius larvae and as a consequence infective copepodids, was from farmed sources. In addition, higher sea water temperatures decreased generation times and increased the rates of development, maturation and potential production of the parasite between 1989 and 1992. It was also reported that the epizootics coincided, geographically and temporally, with a drop in marine survival of post-smolt and adult sea trout in the areas concerned (Whelan, 1993) and that sea trout caught in estuaries sharing the same embayment had similar infestation levels.

Evidence from further afield

The sea lice infestation pattern which characterised the sea trout stock collapse as described by Tully and Whelan (1993) and the premature return of sea trout post- smolts had not previously been recorded in the literature. For a number of years it appeared from the peer reviewed literature as if the events recorded by the Irish workers were unique and confined to the west coast of Ireland, although there were anecdotal reports of similar occurrences. However, by the mid to late 1990s evidence for the occurrence of prematurely returning lice-infested sea trout and char, outside of the west coast of Ireland, was provided by Birkeland and Jakobsen, (1997), Grimnes, (1999) and later by Bjorn *et al*. (2001, 2002 and 2006) from Norway and by Butler and Watt, (2002) and Hatton-Ellis *et al* (2006) from Scotland.

In Scotland from the late 1980s the declared catches of salmon and sea trout declined steeply in some of the west coast fisheries. The average annual declared catch of salmon and sea trout in the North West and West Coast Statistical Regions in the period 1970 – 1980 was 11,846. Over the period 1990 – 2000 this figure had declined by 47% to 6,312. This decline was coincident with the expansion of salmon farming in this area and there was growing concern that sea lice emanating from the farms could be impacting on the migrating smolts. The Association of West Coast Rivers Trusts carried out intensive monitoring of sea lice levels on sea trout over the period 1998 to 2000 and found that localised epizootics occurred every year of the survey and these coincided with the presence of ovigerous lice on farms. In areas of mixed year class production on farms, epizootics were evident every spring, but occurred every second spring in areas of single year class production. In 1998 – 2000 at least 14 - 40% of sea trout were infected

with potentially lethal infestations of lice (Butler, 2002). Low smolt-finnock marine survival rates were also recorded from the River Tournaig (0.8% to 8.1%) and from the River Shieldaig (1.0% to 4.6%), Butler and Walker (2006).

Evidence for the premature return of sea trout post-smolts was provided from trapping experiments on the Shieldaig River, which commenced in 1999. Tagging experiments showed that heavy infestations of lice may rapidly occur once sea trout post-smolts enter salt water. Six prematurely returned, tagged post-smolts, carried 20 - 977 juvenile lice after maximum periods of 5 to 15 days at sea. One fish returned with an infestation of 436 lice after five days and another had 977 lice attached after 15 days (Hatton-Ellis *et al*., 2006).

A sea trout tracking study carried out on Loch Ewe (Johnstone *et al*., 1995) suggested for the first time that major sites for infection of post-smolts with sea lice could be in shallow estuarine conditions among marine algae. The study also suggested that variation in the movement patterns of sea trout between and within sites sampled might help to explain some of the large variation in sea lice infestation levels on the sea trout sampled.

A field experiment conducted by Birkeland and Jakobsen (1997) in the River Lønningdalselven in spring 1992 supported the hypothesis that *L. salmonis*, infestations may cause premature return of sea trout juveniles, either to estuaries or to rivers. When lice-infested (exposed) and un-infested (control) sea trout post-smolts were released simultaneously into the sea, exposed fish returned to the estuarine area earlier compared with controls. Within the following two days, exposed sea trout migrated further into fresh water. No sea trout returned to the fish trap later than day four, and none of the Atlantic salmon juveniles that were released returned to fresh water.

This study supported the hypothesis that salmon lice infestations may induce migration of sea trout juveniles, either to estuaries or to rivers. The fish were infested with a median of 62.5 lice, dominated by chalimus larvae and late juveniles. After release, sea trout juveniles had the possibility to disperse into large areas in the sea. However, more than 60% of the lice-infested smolts returned to the small estuarine area on the day of release, compared with only 3% from the unexposed control group. Thus, separately released groups of exposed sea trout migrated towards the river outlet while control fish swam to other areas. This result corresponded with Irish and Norwegian field observations, (Tully *et al*., 1993; Birkeland, 1997). Blood samples collected from the fish just before release suggested that exposed fish suffered from severe osmoregulatory problems. Exposed fish had higher levels of chloride and lower levels of albumin and total protein relative to unexposed control fish.

Timing and pattern of infestation

Bjorn *et al*. (2001 and 2002) investigated the abundance of salmon lice on two stocks of sympatric or over-lapping populations of anadromous arctic char and sea trout, in sub-Arctic regions in northern Norway, in June, July, and August 1992 and 1993. Salmon lice infestation levels on both species differed significantly between areas with intensive salmon farming activity (exposed locality), and areas with very limited activity (unexposed locality). Levels also differed between years and between weeks within the same year. The 1992 and 1993 infestation pattern in the exposed area showed an epidemic tendency in both arctic char and sea trout, characterised by a sudden increase in both prevalence and abundance of lice larvae in July 1992 (23.6 - 25.7 lice/fish) and August 1993 (19.9 - 20.8 lice/fish). Maximum lice counts from the exposed locality exceeded 200 lice larvae per fish but few older lice, while fish in the unexposed locality carried on average less than ten lice of all developmental stages (Bjørn *et al*., 2001).

The authors noted that other studies had confirmed that the infestation pressure on wild sea trout (Grimnes *et al*., 1999, 2000) and farmed Atlantic salmon (Boxaspen, 1997; Jackson *et al*., 1997) differed between years. Grimnes *et al*. (1999) showed that the infestation on wild sea trout at the exposed locality in Nordland County in 1998 was only 10–20% of that reported by Bjørn *et al*. (2001) for the same locality in 1997. Moreover, heavy infestations of lice larvae were not observed until September in 1998 (Grimnes *et al*., 1999), whereas they were appearing already in June the previous year.

In a further series of studies, Bjørn examined temporal changes in lice infestation patterns and how the impact of the lice may vary amongst different species in Norway. Bjørn *et al.* (2006) showed that sea trout and arctic char 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 frequently found during August. No Atlantic salmon post-smolts were found to be 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. This pattern of infestation was also noted from northern fjords by Bjørn and Finstad, 2002

These observations indicate that Atlantic salmon in Norway, which migrate to sea as smolts during a relatively confined period in late June / July, may or may not encounter peak sea lice production in the northern fjords. In contrast, sea trout and arctic char 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 char 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.

In contrast Poole, Nolan and Tully (2000) showed in their Clew Bay (Ireland) study that heaviest infestation and highest estimated blood cortisol occurred at the first sampling date (21st May). At this time of year, in southern latitudes, post-smolts are adapting to salt water and endogenous cortisol levels, associated with sea water adaptation, are high.

Variability in lice infestation levels between years, however, seems to be less in farm-free southern areas (Tingley *et al*., 1997; Schram *et al*., 1998), and probably represents a "stable" situation with few adverse effects on the fish (Tingley *et al*., 1997).

As pointed out by Costello (2006) transmission of mobile stages between hosts may also be an important mechanism for sustaining lice numbers but is largely unstudied. It would enable redistribution of lice among hosts so as to prevent pathology, which would lead to host mortality and loss of lice habitat. By increasing the number of hosts infested, it would further spread the lice population. This is most likely to be an issue in confined situations such as within a salmon farm site or where there is an escape of adult farmed fish.

Sources of sea lice

The work of Heuch and Mo (2001) supported previous work by Tully and Whelan (1993) when their studies in Norway concluded that total lice egg production annually in farming areas increased by more than 50 times compared to pre-farming conditions. They also stated that years with optimal biotic and abiotic conditions would result in a large production of lice larvae from farmed salmon and that these are probably the main cause of the lice epidemics observed on wild sea trout in farming areas (Tully *et al*., 1999; Bjørn *et al*., 2001). As was the case in Ireland and Scotland (Tully *et al*., 1993; Butler and Watt, 2002) such epidemics were characterised by a sudden, heavy infestation with lice larvae, premature return to fresh water of heavily infested fish, and no accumulation and development of the lice population on captured fish with time. Butler (2002) concluded that in Scottish waters less than 1% of the sea lice originated from wild salmonids.

Dispersion of lice larvae

The relationship between sea lice infestation on sea trout and distance to aquaculture sites was examined by Tully *et al.* (1999) and Gargan *et al.* (2003). This latter study (a 10 year study which comprised data from 4,600 sea trout) demonstrated a statistically significant relationship between lice infestation on sea trout and distance to the nearest salmon farm, with highest infestations and variation in infestation at sites less than 20km from farms. The mean total lice infestation was lower at sites between 20 - 30 km from farms, and beyond 30 km, very low mean lice levels were recorded. Chalimus lice stages dominated the sea lice population structure at distances of < 20 and 20 - 30km.; at distances <60 and <100 km, chalimus and post chalimus were equally

represented; and at sites > 100km post chalimus stages predominated. Regression of log-transformed data for individual years showed significant relationships in all years except 1994 and 1999, although substantial variation existed in the data, particularly close to farms.

The authors suggested that the process of dispersal of lice from farms, the actual lice production from farms and the mechanism by which these larvae are transmitted to sea trout may differ at each site. This finding is not unexpected given the different hydrodynamics, topography, salinity variation and behaviour of trout across the sites in question.

A more general review of dispersal distances of larvae of other marine species in relation to the typical range of coastal ocean current conditions further suggested that lice larvae may be transported an average of 27 km (11 – 45 km range) over 5 – 15 days, depending on current velocity (Costello, 2006).

Locating the infective stages of sea lice

While detailed studies were carried out in Norway, Ireland and Scotland describing larval distribution patterns and host infestation levels of *L. salmonis* (Costelloe, Costelloe & Roche, 1995; Costelloe, Costelloe & Roche, 1996; Gravil, 1996; Costelloe, Costelloe, Coghlan, O'Donohoe & O'Connor, 1998a; Costelloe, Costelloe, O'Donohoe, Coghlan, Oonk & Van Der Heijden, 1998b; O'Donoghue, Costelloe & Costelloe, 1998, Butler, 2002) it proved very difficult to consistently locate sea lice larvae within inner estuaries. These findings led initially to the suggestion that there was a very high retention of sea lice within fish farm cages and those lice found close to river mouths came from wild salmon and sea trout (Costelloe *et al*., 1996; Gravil 1996).

The first published evidence for the presence of infective stages of sea lice in inner bays or estuaries was provided by McKibben and Hay (2004) who examined the relative density of *L. salmonis* larvae in the inter-tidal areas of Loch Torridon in Scotland. Samples of larval sea lice were obtained year round, at approximately weekly intervals, from a 50m transect at the mouth of the River Shieldaig, from March 2001 to June 2003, and compared with frequencies of gravid female sea lice on the two local salmon farms. Their study found that the infectious stage of *L. salmonis* could be successfully located close to river mouths using plankton sampling. Copepodids were present in high numbers over a sustained period and were abundant in the early spring at times when salmon and sea trout smolts go to sea. High levels of copepodids were also found during the winter months of November and December. No planktonic sea lice were found along their sampling transect when gravid females were not present on the local fish farms.

Several studies have shown that the age structure of the louse on individual fish is generally restricted to a few life stages proximal to each other in life cycle, indicating that transmission of the parasite to individual fish occurred very soon after entry into the sea (Tully *et al*., 1993; Birkeland & Jacobsen, 1997; MacKenzie *et al*., 1998 McKibben & Hay, 2004). Thus, it would seem probable that the first substantial site of infection is in or near the inter-tidal zone. In the case of the study carried out by McKibben & Hay (2004) the major concentrations of sea lice were primarily located close to the river mouth rather than being dispersed along the shores of Loch Shieldaig.

As outlined above, Costelloe *et al*. (1995, 1996) concluded that the low densities of sea lice found outside fish farm cages indicated that there was low dispersal from the cage to the outside environment. They concluded that there was a high retention of sea lice within the cages and a high dispersal rate outside of the cage and therefore the copepodids found in the inner estuaries could not have come from the salmon farm. However, the McKibben and Hay study confirmed earlier work from the River Shieldaig (Hatton-Ellis *et al*, 2006) and showed a marked inter-annual divergence between the samples taken in the first year of production (2000 and 2002) and those taken in the second year of production (1999, 2001 and 2003) with sea lice copepodids only being found in the plankton samples when gravid female sea lice were present on local fish farms. In contrast to the conclusions reached by Costelloe *et al*. (1995 & 1996) the lack of larval sea lice in alternate years suggests that the source of these lice was not from wild fish but was of fish farm origin. The distances between the nearest fish farms and shoreline sampling sites suggested that larval sea lice were dispersed over distances of at least 4.6 km. The authors also pointed out

that during the study period no wild salmon entered the Shieldaig fish trap and stated that it was most unlikely that the sea lice larvae were originating from adult lice on wild fish.

Middlemas *et al*. (2010) carried out further work on Loch Shieldaig over five successive fish farm cycles from 2000 to 2009. They also found that lice levels were generally higher on salmon farms during the second year of two-year production cycles and that the percentage of sea trout with lice, and those above a critical level for survival, were significantly higher in the second year of a two-year production cycle (Revie *et al*., 2002; Lees *et al*., 2008). These patterns were consistent with what was found in 2002 – 2003 across the Scottish west coast. Middlemas *et al*. (2010) concluded that the results suggest a link between salmon farms and sea lice burdens on sea trout in the west of Scotland and add to the evidence from a number of countries that, in general, the sea lice burdens of wild sea trout are related to the presence of salmon farming.

Dispersion models

While the work of McKibben and Hay (2004) clearly demonstrated the presence of sea lice larvae in the inter-tidal areas of Loch Torridon it was still not clear how the lice were carried into these areas. As outlined previously, Costello (2006) was the first to suggest a model of how larvae of *L. salmonis* may be transported to intercept migrating salmonid hosts and proposed that copepodids swim to the surface during daylight where the onshore wind moves the surface water towards the shore and into estuaries. Gillibrand & Willis (2007) mathematically demonstrated such a model for the dispersal of sea lice larvae under typical coastal environmental conditions (including tidal, riverine and wind-driven currents) and showed that inclusion of larval behaviour in the model best explained field observations of copepodid distribution. In addition, their hydrographic model showed that, below the seaward freshwater current, is an upstream mid-depth current that can transport larvae towards land and into estuaries. Naturally, variation in wind force and direction owing to weather conditions and landscape, and in current speed and direction owing to seabed topography, will further affect water movement and larval dispersal (Amundrud & Murray, 2009).

While the presence of *L. salmonis* chalimi on Atlantic and Pacific salmon, sampled in offshore seas, indicates that infestation may occur there, the most significant infestations will occur in coastal waters owing to the congregation of hosts, larval behaviour and hydrography. The timing of salmonid migrations is important in *L. salmonis* infestations and is similar in both the Atlantic and Pacific Oceans. Juvenile salmon migrate from rivers to the sea in spring (mainly April to May), whereas adults primarily return to the coast during the summer (mainly June to October) before entering the rivers to spawn; where attached lice will die in fresh water (Dill *et al*., 2009). Thus juvenile fish will suffer less exposure to lice transferred from returning adults the sooner they migrate away from the coast, a situation called migratory allopatry between host and parasite (Krkošek *et al*., 2007a).

Conclusions

As outlined above the debate regarding the impacts of sea lice on wild salmonids and the role fish farms play in exacerbating such problems has raged for over twenty years. Until relatively recently it was not clear that a satisfactory scientific resolution of the issues raised by the debate had been found.

Scientists were constantly challenged to find clear indicators of whether juvenile lice on wild fish had come from farmed fish but their efforts met with little success. Although it is possible to distinguish lice from farmed and wild fish using stable isotopes, elemental signatures and colourants derived from feeding on farmed fishes, these indicators do not identify farm lice progeny that may infect wild fish (Todd, 2006). Genetic analyses indicate that *L. salmonis* is one well-mixed population across the North Atlantic, but that there has been some genetic drift from the North Pacific population; thus genetics are unlikely to distinguish farm and wild host populations (Costello, 2006; Todd, 2006).

To date it has proved impossible to carry out direct observations and tracking of individual sea lice larvae from release by the adult female to ultimate settlement on a host fish. This led Bjørn (2007) to conclude that direct evidence of louse transfer from farmed to wild hosts has not been found. Scientists therefore adopted alternative indirect analytical approaches to specifically assess farm-wild interactions. (Revie *et al*., 2009). These techniques involved collating data on a broad range of related issues such as infestation parameters, correlations between farm activity and the occurrence of juvenile lice on host species in the water column, and the development of spatial transmission models. Despite their limitations, such indirect studies have provided a wealth of evidence linking localised epizootics of juvenile lice with increased lice levels on migratory salmonids in these areas. (Bjørn *et al*., 2001b; Gargan *et al*., 2003; Krkošek *et al*., 2005).

Within Atlantic salmon farms, or within fish-farming areas, large numbers of hosts are continually present, facilitating substantial build-up of reproducing female lice and a continuous possibility of re-infestation (e.g. Tully and Whelan, 1993; Heuch and Mo, 2001). Due to the elevated number of salmon hosts, the potential for sea lice larval production is substantially higher under marine cage-culture conditions (Heuch *et al*., 2005).

Salmon louse epidemics in wild salmonids may occur in years when optimal conditions for louse reproduction and dispersal are present, (Bjørn *et al*., 2001b: Stien *et al*., 2005). At least in sea trout populations, these epidemics are characterised 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).

Bjørn also noted that the risk to wild salmonids of infestation from free-swimming salmon-louse copepodids, derived from cultured fish, is very variable. It 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). He also pointed out that the risks of salmon louse infestation may, therefore, also differ between salmonid species (e.g. between Atlantic salmon and sea trout), depending on their migratory behaviour and the local conditions at the time of migration.

Revie *et al.,* 2009 concluded that while it is not plausible to draw a single over-riding conclusion regarding the potential negative impacts of sea lice on all wild fish stocks world-wide, the weight of evidence is that sea lice of farm origin can present, in some locations and for some host species populations, a significant threat. Hence, a concerted precautionary approach both to sea lice control throughout the aquaculture industry and to the management of farm interactions with wild salmonids is expedient.

More recently Costello (2009) carried out a very detailed review of the impacts of sea lice from salmon farms on wild salmonids in Europe and North America. He concluded that there was compelling evidence that lice from farms are a significant cause of mortality in nearby wild fish

populations. Amongst the key pieces of evidence he quotes in support of his conclusion are the following:

"Sea lice epizootics (exceptionally heavy and fatal infestations) appear to be rare in wild fish populations. However, it is possible that heavily infested fishes die and are not observed, and evidence from wild fish species, including salmonids, suggests that pathogenicity may occur naturally (Costello, 1993, 2006; Hvidsten *et al*., 2007). In 1989, sea lice epizootics were recorded on wild sea trout, *Salmo trutta* L., in Ireland for the first time, and it was proposed that salmon farms were the primary source (Tully & Whelan, 1993). Similar epizootics were found on wild salmonid species in Scotland, Norway and British Columbia, including sea trout, char, *Salvelinus alpinus* (L.) and pink salmon *Oncorhynchus gorbuscha* (Walbaum). In all cases, they only occurred in regions where Atlantic salmon was farmed in net pens (e.g. Tully *et al*., 1999; Butler, 2002; Gargan *et al*., 2003; Krkošek *et al*., 2005, 2006b; Morton *et al*., 2004, 2005) and were characterized by heavy infestations of chalimi. In Europe, epizootics were also characterized by the premature return of the juvenile sea trout to fresh water (Birkeland, 1996; Gargan *et al*., 2003; Hatton-Ellis *et al*., 2006)".

"Recently, a series of papers by independent groups of researchers from different countries have provided models and data of how lice infestations can occur for the salmon louse, *L. salmonis*. This marks a milestone in understanding the ecology of sea lice, but perhaps more importantly, in how aquaculture may impact on wild fish populations".

"The most significant progress in the understanding of sea lice in recent years has been the new data on larval dispersal, associated with oceanographic, mathematical and conceptual models".

"Thus, at least in, Europe, empirical data indicated that the infective copepodids of *L. salmonis* concentrated in the path of migrating salmonids in estuaries. However, whether these copepodids arose from salmon entering rivers to spawn, escaped farm fishes, farms or wild fishes further offshore, was uncertain. Since then, extensive plankton surveys in a Scottish sea loch supporting a wild salmon population have indicated that gravid *L. salmonis* on farmed salmon were the major contributor to sea lice larvae recovered from the plankton (Penston *et al*., 2008 a, b; Penston & Davies, 2009)".

"Gillibrand & Willis (2007) mathematically demonstrated such a model for the dispersal of sea lice larvae under typical coastal environmental conditions (including tidal, riverine and wind-driven currents) and showed that inclusion of larval behaviour in the model best explained field observations of copepodid distribution. In addition, their hydrographic model showed how below the seaward fresh water current is an upstream mid-depth current that can transport larvae towards land and into estuaries. While some model studies (e.g. Brooks & Stucchi, 2006; Gillibrand & Willis, 2007) suggested that lice larvae could be washed out of inlets during high freshwater flows, other models found that gyres within sea lochs could retain larvae (Gillibrand & Amundrud, 2007). Importantly, such models may be misleading if larvae avoid entrainment in fresh water as laboratory experiments indicate. Larvae may thereby avoid salinity-delayed development or mortality, and seaward transport, and be retained in the inner estuaries as plankton sampling suggests (Amundrud & Murray, 2009). Naturally, variation in wind force and direction owing to weather conditions and landscape, and in current speed and direction owing to seabed topography, will further affect water movement and larval dispersal. Whether a freshwater current is present or absent, wind-driven surface currents are critical in larval dispersal (Amundrud & Murray 2009). Penston *et al*., (2008b) sampled plankton at 0 and 5m depth (in the absence of a freshwater surface layer) and found sea lice nauplii most abundant at 5 m, but copepodids at the surface. Thus copepodids would be subjected to dispersal by wind-driven surface currents, and nauplii most abundant near their sources (e.g. farms), as Costelloe *et al*., (1995) found in Ireland and Penston *et al*., (2008a &b) in Scotland".

"The evidence that salmon farms are the most significant source of the epizootics of sea lice on juvenile wild salmonids in Europe and North America is now convincing (Heuch *et al*., 2005; Costello, 2006; Krkošek *et al*., 2006b, 2007a & b; Todd, 2006). Farms may contain millions of fishes almost year round in coastal waters and, unless lice control is effective, may provide a continuous source of sea lice, although the amount of infestation pressure will vary over time owing to seasonal and farm management practices (e.g. fallowing). If escaped farm fishes remain in

coastal waters, they will be an additional reservoir of lice. Experimental and field data in conjunction with mathematical models provide an explanation of how the larvae of the most common and pathogenic species, *L. salmonis*, disperse and congregate to infest wild salmonids in coastal waters. The correlation of epizootics on wild fishes in areas with fish farms, compared with (control) areas without farms, has been repeated over years and in different countries."

"Not all salmon farms have sea lice problems, and local hydrographic conditions vary and will influence larval dispersal. Despite improved knowledge about how to control sea lice on farms, including fallowing and a wider range of parasiticides, sea lice epizootics persist. Some salmon farms will not be a source of sea lice for wild fishes, and epizootics may not always occur in areas with salmon farms".

In contrast, Revie *et al.* (2009) draw more tentative conclusions : "…….. the evidence is largely indirect or circumstantial that sea lice emanating from salmon farms can and do exert detrimental effects on wild salmonids. That is not to denigrate or detract from the quality of the various observational, experimental and theoretical approaches adopted by scientists in addressing this important environmental issue. Rather, it is an objective acknowledgment that it is practically impossible to precisely quantify wild-to-farm versus farm-to-wild and wild-wild infestation interactions".

This review has clearly shown that in fish farming areas, sea lice epizootics have been recorded from a wide range of bays, sea lochs and fjords throughout Ireland, Scotland and Norway, over the past 20 years. These larvae may infest neighbouring migratory salmonid populations as copepodids and have often been recorded as later stage chalimi larvae. In areas not affected by such epizootics salmonids display lower lice burdens characterised by lice at a later stage in their development, often pre-adult and adult lice. The pattern of infestation is variable over time and space and very much influenced by local environmental conditions and the management practices in place on the farms. It has also been shown that in bays holding one generation of farmed salmon epizootics occur every second year whereas in a bay containing mixed generations epizootics may occur sequentially.

Although impacts on individual fish, particularly sea trout and char in the case of Norway, have been consistently reported it has generally proved very difficult to relate these to impacts at a population level or to estimate the percentage of mortality in any given year that is attributable to lice infestation from neighbouring farms. Trap census data from the Burrishoole index system in Ireland and from trapping stations on the Gowla and Inver systems have clearly shown exceptionally poor marine survival in tandem with heavy sea lice infestations but it again proved difficult to show the proportion of the additional mortality attributable to lice from the neighbouring salmon farms (Poole *et al*., 1996 and Gargan *et al*., 2003 and 2006)

Much of the published data relates to studies of sea trout and char since the migratory behaviour of Atlantic salmon smolts, their relatively long absence from inshore areas while feeding at sea and increasing evidence of high seas marine mortality factors, make the study of near shore post-smolt mortality factors far more problematic. However, Finstad *et al.* (2000) and Hvidsten *et al.* (2007) have shown that Atlantic salmon post-smolts may be infested initially by salmon lice during their migration through fjords and outer coastal areas. Norwegian investigations in the early 1990s indicated that infestation of sea lice larvae occurred on Atlantic salmon post-smolts descending the long and intensively farmed fjords of western and central Norway (Finstad *et al*., 1994, 2000; Holst *et al*., 2003) and direct parasite-induced mortality in Atlantic salmon post-smolts has been predicted to vary between 0 and 95% among years and fjords of the intensively farmed area of western Norway (Holst *et al*., 2003; Bjørn *et al*., 2009).

Recent studies on larval dispersal, associated with oceanographic, mathematical and conceptual models and studies linking the abundance of juvenile lice in inner estuaries with abundance on neighbouring farms, have provided for the first time a clear understanding of how migratory salmonids could be infested by juvenile lice from salmon farms. Results of the studies quoted previously highlight the importance of wind-driven circulation for larval lice transport and suggest that local environmental conditions have considerable impact on the probability of sea lice infection spreading between wild and farmed fish populations. However it is the sub-littoral

regions around the boundary of elongated inlets which are more likely to contain elevated levels of copepodids.

The transportation of the copepodids along the halocline, the very area where salmonid smolts adapting to saltwater are most likely to be encountered in spring, provides a very satisfactory explanation of how they may well encounter a greater infestation pressure during epizootics.

The recently developed transportation models have mapped the potential spread of sea lice using a three dimensional hydrographic model, coupled with a biophysical particle tracking model to trace the dispersion of sea lice from points representing farm sites. It is clear from the research carried out to date that understanding the hydrodynamics of specific bays or estuaries where fish farming is taking place and linking this with parameters relating to local wind conditions is key to predicting the likely impact of an epizootic on the inner areas of an embayment. Equally important is a more detailed knowledge of the ecology of the sea louse and how it will react to increasing temperatures as predicted under various climate change scenarios.

The functional lice dispersion models now available make it possible to move from research which focused primarily on the source of the lice epizootics to the provision of additional tools for the assessment of the scale of potential problems in individual bays and methodologies to assess the efficacy of a range of lice management protocols for use in marine salmonid culture.

Acknowledgments

Grateful thanks are due to my many colleagues who generously provided published material for the review and assisted with its compilation.

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